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September 1989

PRAIRIE BASIN WETLANDS OF THE DAKOTAS: A COMMUNITY PROFILE

Fish and Wildlife Service

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Cover:

Upper left: Palustrine emergent vegetation (*Scirpus acutus*) in an oligosaline, semipermanently flooded wetland.

Upper middle: Palustrine aquatic bed vegetation (*Potamogeton gramineus*) in a fresh, seasonally flooded prairie wetland.

Upper right: Snow geese (*Chen caerulescens*) using a cultivated, temporarily flooded wetland during spring migration through the Prairie Pothole region.

Bottom: Basin wetlands of various sizes and with different hydrological regimes are a major feature of the landscape in croplands, haylands, and pasture types of land-use patterns in the Prairie Pothole region.

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PRAIRIE BASIN WETLANDS OF THE DAKOTAS: A COMMUNITY PROFILE

by

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PREFACE

This description of prairie basin wetlands of the Dakotas is part of a series of community profiles on ecologically important wetlands of national significance. The shallow wetlands of the Dakotas form the bulk of the portion of the Prairie Pothole Region lying within the United States. This region is famous as the producer of at least half of North America's waterfowl and an unknown, but large, proportion of other prairie-dwelling marsh and aquatic birds.

The wetlands described here lie in relatively small, shallow basins that vary greatly in their ability to maintain surface water, and in their water chemistry, which varies from fresh to hypersaline. These wetlands occur in a wide variety of hydrological settings, in an area where annual and seasonal precipitation varies greatly in form and amount. Thus the presence of surface water in these wetlands is largely unpredictable. Superimposed on these phenomena are the effects of a variety of land uses, including pasture, cultivation, mechanical forage removal, idle conditions and burning. All those factors greatly affect the plant and animal communities found in these basins.

This profile covers lacustrine and palustrine basins with temporarily flooded, seasonally flooded, and semipermanently flooded water regimes. Basins with these water regimes compose about 90% of the basins in the Prairie Pothole Region of the Dakotas. This profile outlines the wetland subsystems, classes and subclasses that occur in these basins, and provides a useful reference to their geologic, climatic, hydrologic, and pedologic setting.

Detailed information on the biotic environment of the wetlands dealt with in this profile will be useful to scientists and resource managers. Special recognition is paid to the macrophyte and invertebrate communities, which have dynamic qualities found in few other of the world's wetland ecosystems.

The most noteworthy animal inhabitants of these basins are waterfowl, which are a resource of international concern. Because of the importance of this resource, much research on the habitat use and feeding ecology of breeding waterfowl has been conducted in the region. These topics receive special attention in this profile.

The Prairie Pothole Region is a major world supplier of cereal grains. Consequently, wetlands in the region are often drained for crop production or otherwise cropped when water conditions permit. These practices degrade the value of wetlands for most species of wildlife and conflict with the aims of conservationists. The subject of human uses and impacts to prairie wetlands is thus an important part of this profile.

CONVERSION TABLE

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
meters (m)	0.5468	fathoms
kilometers (km)	0.6214	statute miles
kilometers (km)	0.5396	nautical miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters (m^3)	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons (t)	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (°C)	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

Multiply	By	To Obtain
inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
statute miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
square miles (mi^2)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28350.0	milligrams
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
pounds (lb)	0.00045	metric tons
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees (°F)	0.5556 (°F - 32)	Celsius degrees

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CHAPTER 1. INTRODUCTION

"The entire face of the country is covered with these shallow lakes, ponds and puddles, many of which are, however, dry or undergoing a process of gradual drying out." So stated Charles Froebel (1870) as he described the lands along the Sheyenne and James River Valleys, Dakota Territory, during General Alfred Sully's 1865 expedition. Thus the uniqueness of North America's Prairie Pothole Region has been recognized for well over 100 years. In this Community Profile, we briefly describe the biotic and abiotic settings and features of the most common kinds of wetlands found in the portion of this region that lies in the Dakotas, and outline the natural and manmade ecological processes that affect these wetlands.

1.1 GEOGRAPHIC AREA COVERED

The Prairie Pothole Region of North America stretches from central Alberta to central Iowa and encompasses well over 700,000 km^2. This community profile covers the 168,000-km^2 portion of the region lying in North and South Dakota (Figure 1). This area is bounded on the north by the International Boundary, east by the Red and Minnesota River Valleys and portions of the western boundaries of Minnesota and Iowa, and on the south and west by headwaters of numerous small streams and rivers along the north and east sides of the Missouri River. A few small areas of potholed land not shown in Figure 1 lie west of the Missouri River.

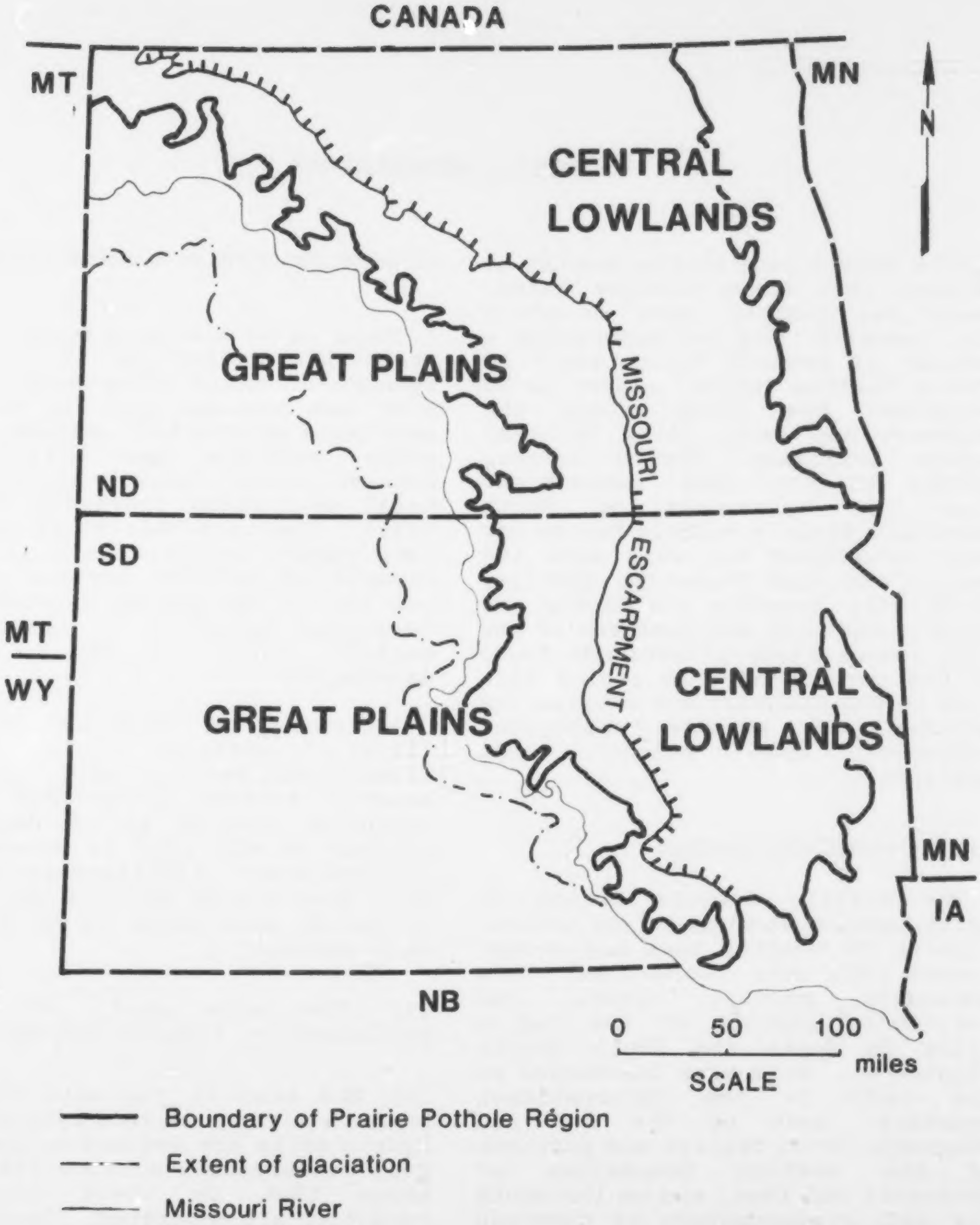
1.2 DEFINITION OF PRAIRIE BASIN WETLANDS

There is no single scientifically acceptable definition of wetlands because of their tremendous diversity and because they lie along a continuum or gradient between deepwater habitats and uplands or between purely aquatic and terrestrial ecosystems (Cowardin et al. 1979). The term "basin" as used in this report refers to a depression capable of holding surface water, but not to the entire watershed or "drainage basin" that contributes surface water runoff to that depression.

According to Cowardin et al. (1979), wetlands are lands transitional between terrestrial and aquatic systems where the water table is usually at or near the surface or the land is covered by shallow water. Additionally, a site must have one or more of the three following attributes to be defined as a wetland:

(1) The site must, at least periodically, support hydrophytes.

(2) The land at the site must be predominantly undrained hydric soil. Hydric soils are defined by the U.S. Soil Conservation Service (1985) as those that in their undrained condition are saturated, flooded, or ponded long enough during the growing season to develop anaerobic conditions favoring the growth and regeneration of hydrophytic vegetation.


CANADA
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MN
N
CENTRAL LOWLANDS
GREAT PLAINS
MISSOURI ESCARPMENT
ND
SD
MT
WY
GREAT PLAINS
CENTRAL LOWLANDS
MN
IA
NB
0
50
100
miles
SCALE
Boundary of Prairie Pothole Région
Extent of glaciation
Missouri River

Figure 1. Prairie Pothole Region of the Dakotas showing relation to maximum extent of glaciation and Missouri River. The Missouri Escarpment separates two major biogeographic regions of North America, the Great Plains, and Central Lowlands (after Bluemle 1977).

(3) The site substrate is nonsoil and is saturated with water or covered by shallow water at some time during the growing season each year. Nonsoils are defined by the U.S. Soil Conservation Service (1975) as barren areas such as ice, rock, or substrates underlying deep water.

Nearly all natural basins in the Prairie Pothole Region of the Dakotas have both the first and second of these attributes, and thus are wetlands according to the Cowardin et al. (1979) classification. The basins are underlain by hydric soils, and when surface water is present, can support hydrophytes. Many of the basins are intensively cultivated; the soil may be bare or commercial crops may be present during dry conditions, but when water is replenished during the growing season, communities of hydrophytes quickly develop.

Few basins in the region contain deep-water habitat. This habitat will not be dealt with in this report. Deep-water habitats are permanently flooded lands lying below the deep-water boundary of wetlands. For the wetlands described in this report, the boundary between them and deep-water habitats lies at a depth of 2 m below low water; however, if emergents, shrubs, or trees grow beyond this depth at any time, their deep-water edge is the boundary. Substrates of deep-water habitat are nonsoil whose water depths are in excess of that required to support emergent vegetation (Cowardin et al. 1979; U.S. Soil Conservation Service, Soil Survey Staff 1975). In addition, a small proportion of the wetlands in the region are of the water regimes "intermittently exposed" and "saturated." These will also be omitted from this report.

Prairie wetlands occur in glacially or postglacially derived basins in the northern grassland biome (see Section 2.1). The basins are roughly round or oval in shape, although it is fairly common to encounter some with relatively convoluted shorelines composed of several bays or peninsulas, or, more rarely, with one or several islands.

1.3 CLASSIFICATION OF PRAIRIE BASIN WETLANDS

Systems and Subsystems

Under the Cowardin et al. (1979) wetland classification, the prairie wetlands referred to in this report are palustrine and lacustrine systems. There are no subsystems in the palustrine system. For the lacustrine system, only the littoral subsystem is dealt with in this report. This subsystem extends from the shoreward boundary to a depth of 2 m below low water or to the maximum extent of nonpersistent emergents, if these grow at depths >2 m. The latter conditions are rare or absent in the pothole region of the Dakotas. An outline of the Cowardin et al. (1979) classification system, as it applies to the Prairie Pothole Region of the Dakotas, is shown in Table 1. Only subclasses dominated by plants are included in Table 1 because these subclasses are by far the most common in the region. Little is known about the animals that dominate unvegetated substrates that are known to exist in several wetland classes found in the region.

Classes

Classes of the palustrine system found in the Prairie Pothole Region of the Dakotas are emergent, aquatic bed, unconsolidated shore, unconsolidated bottom, forested, and shrub-scrub. Classes of lacustrine system represented are aquatic bed, emergent wetland, unconsolidated shore, unconsolidated bottom, and rocky shore.

Emergent wetland. This class of wetland, containing erect rooted herbaceous hydrophytes, is by far the most common wetland class in the region. Emergent wetland supports

Table 1. Wetland systems, subsystems, classes, and subclasses of Cowardin et al. (1979) that occur in the Prairie Pothole Region of the Dakotas, and for which dominance types are plants.

System	Subsystem	Class	Subclass
Riverine	Lower Perennial	Aquatic Bed	Algal
			Aquatic Moss
			Rooted Vascular
			Floating
		Unconsolidated Shore	Vegetated
		Emergent Wetland	Non-persistent
	Upper Perennial	Aquatic Bed	Algal
			Aquatic Moss
			Rooted Vascular
			Floating
		Unconsolidated Shore	Vegetated
	Intermittent	Streambed	Vegetated
Lacustrine	Limnetic	Aquatic Bed	Algal
			Aquatic Moss
			Rooted Vascular
			Floating
	Littoral	Aquatic Bed	Algal
			Aquatic Moss
			Rooted Vascular
			Floating
		Emergent Wetland	Non-persistent
Palustrine	(no subsystems)	Aquatic Bed	Algal*
			Aquatic Moss*
			Rooted Vascular*
			Floating*
		Unconsolidated Shore	Vegetated
		Moss-Lichen Wetland	Moss
			Lichen
		Emergent Wetland	Persistent*
			Non-persistent*
		Scrub-Shrub Wetland	Broad-leaved Deciduous
		Forested Wetland	Broad-leaved Deciduous

*See Appendix B for common dominance types.

vegetation that is largely perennial, and present during most of the growing season most years. Emergent wetland is often called marsh, meadow, fen, slough, or swamp in the region. Persistent emergents are by far the most common, although under disturbances such as heavy grazing or cultivation, nonpersistent emergents can dominate.

Aquatic bed. The class "aquatic bed" includes wetland dominated by plants that grow principally on or below the water surface for most of the growing season during most years. This is the second most common wetland class in the region.

Unconsolidated shore. This class is mostly associated with the erosional and depositional shoreline zones of wetlands not dealt with in this report, but the class commonly occurs in many shallow prairie wetlands as bottoms are exposed during drought.

Unconsolidated bottom. This class is mostly associated with the unstable bottoms of wetlands with more permanent water regimes than are dealt with in this report, but can occur in some deeper prairie wetlands as bottoms are exposed during extreme drought.

Scrub-shrub. The class "scrub-shrub" includes wetlands dominated by woody vegetation <6 m tall. In prairie wetlands, this class is mostly limited to temporarily flooded sites long protected from fire and grazing by domestic livestock.

Forested. The class "forested" includes wetlands dominated by woody vegetation 6 m or more tall. In prairie wetland, this class is mostly limited to temporarily flooded sites long protected from fire and grazing by domestic livestock. The class can sometimes develop where artificial disturbance creates sites favorable to germination and growth of seeds from trees with wind-disseminated propagules.

Rocky shore. This class is found only on a few large wetlands in the Prairie Pothole Region where glacial slumping and ice action have strewn boulders along high-energy shorelines. This class is seldom found in the wetlands dealt with in this report.

Water Regimes

The water regimes dealt with in this report are temporarily flooded, seasonally flooded, and semipermanently flooded. Basins where the central or deepest portion is subject to these water regimes compose nearly 90% of all basins in the Prairie Pothole Region. The concentric pattern of these regimes in lacustrine and palustrine wetland systems is shown in Figure 2.

In the basins considered in this report, "emergent wetland" occurs with water regimes temporarily flooded, seasonally flooded, and semipermanently flooded. Water regimes of scrub-shrub and forested wetland are restricted to temporarily flooded areas. Aquatic bed is seasonally or semipermanently flooded. Unconsolidated shore is seasonally or temporarily flooded, but the water regime of unconsolidated bottom is restricted to semipermanently flooded.

Subclasses

Emergent wetland contains vegetation of the subclasses persistent or nonpersistent. "Persistent" vegetation in prairie wetlands is normally perennial in habit and remains standing at least until the beginning of the next growing season. Persistent vegetation is the predominant subclass in nearly all prairie wetlands, often referred to as "wet grasslands." Nearly always annual in habit, "nonpersistent" vegetation increases with falling water levels and disturbance in prairie wetlands.

Aquatic bed can include the subclasses "algal," "aquatic moss," "rooted vascular," or floating. "Rooted vascular" is the predominant subclass because the highly mineralized and alkaline waters of the region are not conducive to the growth of most mosses, and the relatively windy conditions that prevail in the region usually move floating algae and vascular floating plants into emergent wetland, where they can appear below the canopy. The subclasses aquatic moss and floating vascular are found most

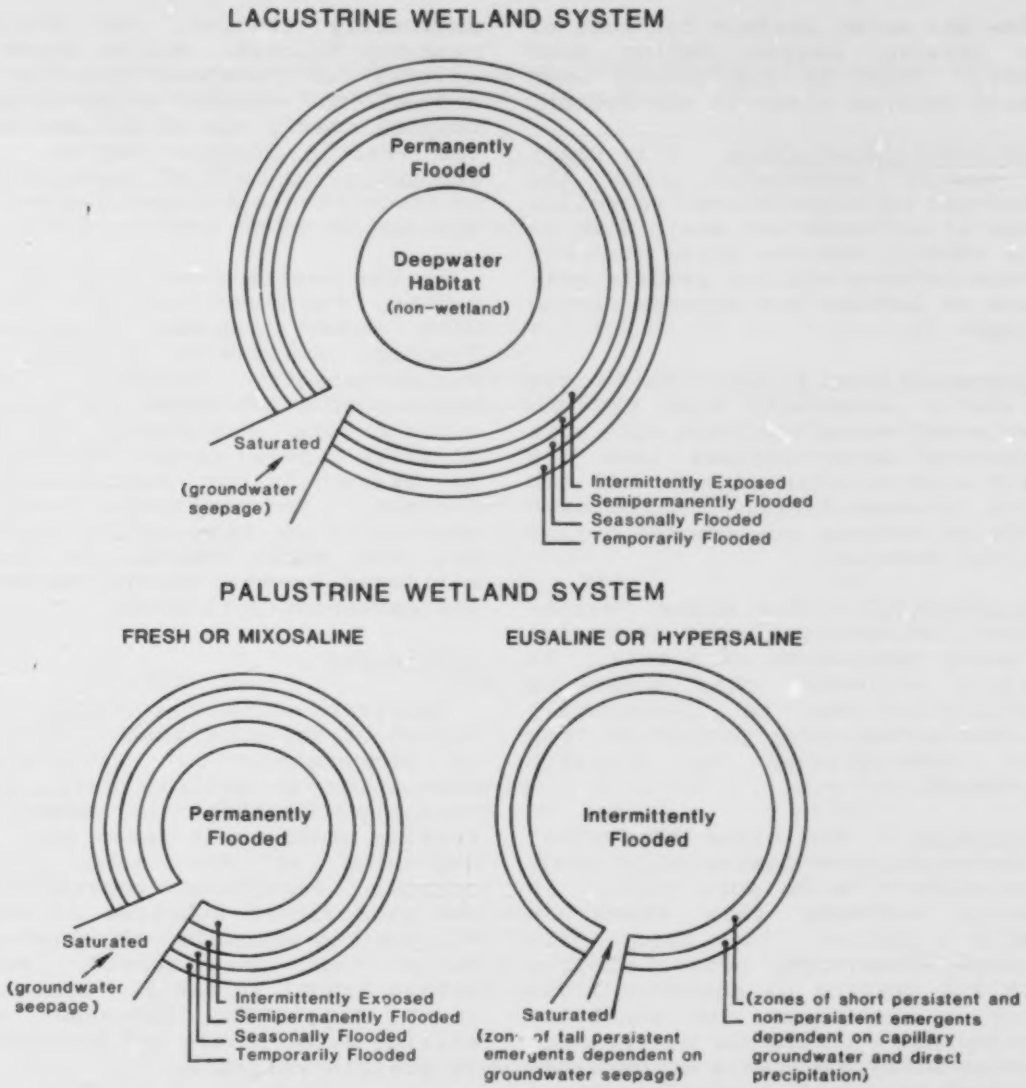

LACUSTRINE WETLAND SYSTEM
Permanently Flooded
Deepwater Habitat (non-wetland)
Saturated
(groundwater seepage)
Intermittently Exposed
Semipermanently Flooded
Seasonally Flooded
Temporarily Flooded
PALUSTRINE WETLAND SYSTEM
FRESH OR MIXOSALINE
EUSALINE OR HYPERSALINE
Permanently Flooded
Saturated
(groundwater seepage)
Intermittently Exposed
Semipermanently Flooded
Seasonally Flooded
Temporarily Flooded
Intermittently Flooded
Saturated
(zones of tall persistent emergents dependent on groundwater seepage)
(zones of short persistent and non-persistent emergents dependent on capillary groundwater and direct precipitation)

Figure 2. Arrangement of Cowardin et al. (1979) water regimes around lacustrine and palustrine wetlands in the Prairie Pothole Region of the Dakotas (from Kantrud et al. 1989).

often in small basins, small bays of larger basins, or openings in emergent wetland, whereas the subclass algal is most often seen in small, highly eutrophic wetlands.

Unconsolidated shore in the wetlands dealt with in this report is usually of the subclass "vegetated." Unconsolidated shore can quickly appear in seasonally flooded wetlands, normally of the class aquatic bed, if drought conditions prevail early in the growing season.

Unconsolidated bottom in the prairie region is usually of the subclasses "sand" or "mud." Areal cover of vegetation in this subclass usually does not exceed 30% (Cowardin et al. 1979). However, in semipermanently flooded wetlands of the Prairie Pothole Region, annuals can germinate and grow to cover values exceeding 30% during years of extreme drought (L.M. Cowardin, Northern Prairie Wildlife Research Center, pers. comm.).

Only the subclasses "broad-leaved deciduous" and "dead" are found in forested and scrub-shrub wetland in the Prairie Pothole Region of the Dakotas.

Relation to Other Wetland Classification

This report includes only information on basins with the temporarily, seasonally, and semipermanently flooded water regimes of Cowardin et al. (1979). These water regimes correspond to those found in the central zones of ponds and lakes classified as temporary (Class 2), seasonal (Class 3), and semipermanent (Class 4) by Stewart and Kantrud (1971). This system was developed specifically for the glaciated prairie region, and unlike the former system, was designed to classify entire basins, rather than the central or concentric peripheral zones or bands of vegetation around the basins that are wetland of differing water regime in the Cowardin et al. (1979) system. The terms "pond" and "lake" usually refer only to the water contained in the basins. Hereafter in this report the terms temporary, seasonal, and semipermanent wetlands will refer to entire basins, and the corresponding zones will be termed wet meadow, shallow marsh, and deep marsh, following Stewart and Kantrud (1971).

Wetland Inventory Maps

Use of the Cowardin et al. (1979) classification system results in large numbers of combinations of wetland system, subsystem, class, and water regime. These combinations are shown as legends (alphanumeric codes) on the National Wetland Inventory maps that are currently being prepared for the United States. Copies of the pamphlet Photointerpretive Conventions for the National Wetlands Inventory (1987), which contains an explanation of these legends, and the status of the wetland mapping effort for the region, is available from the U.S. Fish and Wildlife Service, Regional Wetlands Coordinator, National Wetlands Inventory, Federal Center, Denver, CO 80225. The legends can be used to locate temporary, seasonal, and semipermanent wetland basins by noting instances where these codes are shown for the deepest or central area of a basin. The maps are intended to show the potential natural vegetation. Thus, cultivated wetlands are designated as emergent even though emergent vegetation may be absent.

Wetland Soils

The soils underlying wetland basins in North Dakota have been classified, and classification is in progress for similar soils in South Dakota (Jimmie Richardson, North Dakota State University, pers. comm.). The development of wetland soils depends strongly on length of flooding, water quality, and the relative position of the basins with respect to the ground-water table, according to Bigler and Richardson (1984), Richardson and Bigler (1984), and Fulton et al. (1986). These sources and other material referenced by them show that temporary and seasonal wetlands are usually recharge areas that receive water from the surrounding uplands by runoff or direct precipitation. Clays are dispersed and carried downward by an abundance of fresh water. This results in highly developed soil profiles with argillic horizons. Soil series observed in these situations include Lindaas and Parnell (Typic Agriaquolls) and Tonka, an Argiaquic Agialboll.

Most semipermanent wetlands in North Dakota are flow-through wetlands that receive ground-water discharge and also recharge the ground water. Evapotranspiration, frost action, and a near-surface water table allow water to move from the wetland body to the soils in the wet meadow. Reducing conditions in the water column aid in mobilizing salts into the wet meadow. Several other little-understood factors result in higher soil salinity in the wet meadow than in the adjacent uplands or the interior zones of the wetland basin. These flow-through wetlands have a large range of salinity, and salinization of the whole wetland occurs in some cases. Soils in these wetlands range from Typic Haplaquolls and Calciaquolls in the wet meadow to dominantly Fluvaquentic Haplaquolls such as the Southham series in the shallow marsh and deep marsh zones (Bigler and Richardson 1984). It is in these basins that drainage followed by tillage often results in crop failure because land salinization occurs as the ground-water system delivers low-quality water to the freshly broken soils (Richardson 1986).

A small number of semipermanent wetlands in North Dakota can be considered discharge wetlands. These are underlain by saline soils such as the poorly developed Minnewaukon and Lallie series (Typic Fluvaquents). If drainage is attempted on these soils, salinization prevents the growth of crops other than hay.

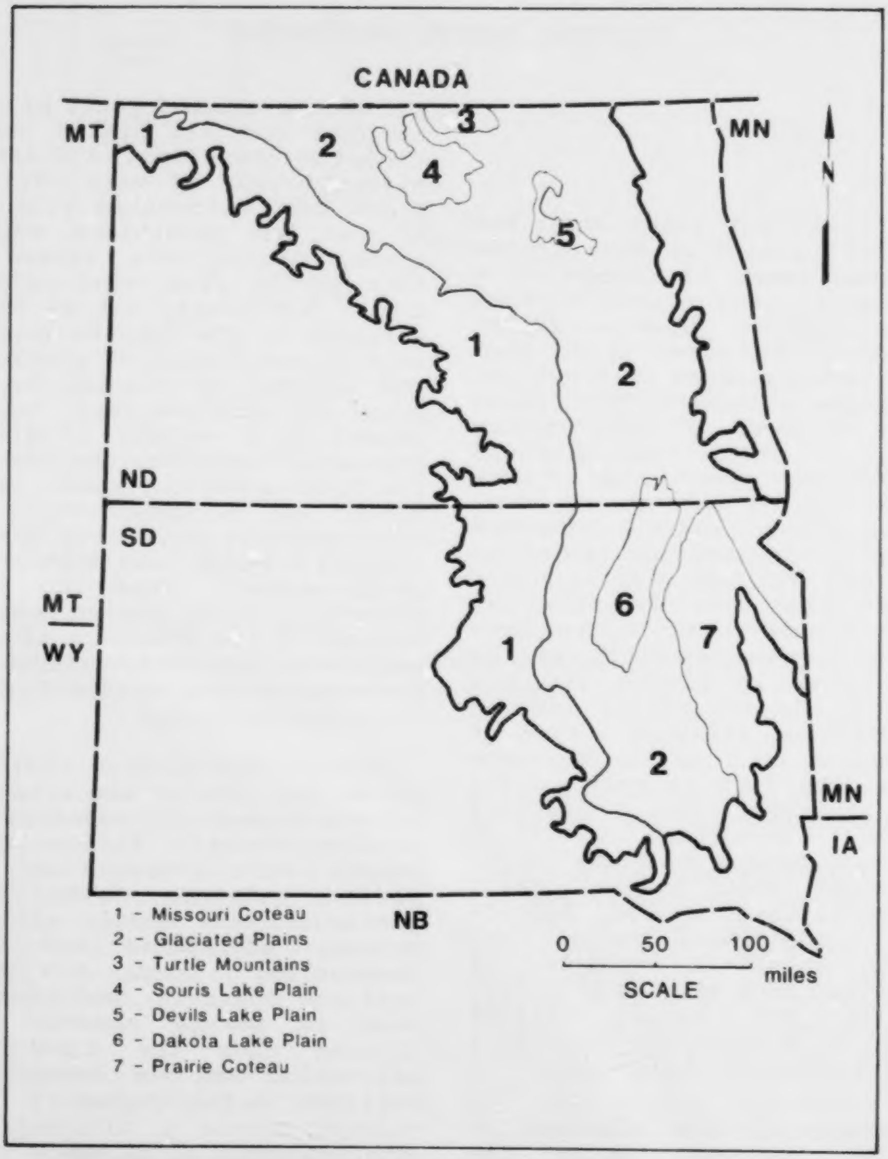
Little is known about heavy metals in soils of prairie wetlands. Martin and Hartman (1984) examined arsenic, cadmium, lead, mercury, and selenium concentrations in sediments of riverine and palustrine wetlands of the North Central United States. Samples from three palustrine wetlands in the Cottonwood Lake area northwest of Jamestown, North Dakota, averaged 6.2 (4.5-9.3), 0.46 (0.42-0.50), 12 (7.4-17), 0.04 (0.02-0.07), and 0.99 (0.43-1.6) mg/kg dry weight of these metals, respectively. Sediments from palustrine wetlands have significantly higher concentrations of arsenic, cadmium, lead, and selenium than those from riverine wetlands, but, with one exception, concentrations were within normal or background ranges.

1.4 DISTRIBUTION AND ABUNDANCE OF WETLANDS

During the 1960's and 1970's, 2.3 million temporary, seasonal, and semipermanent wetland basins, with a total area of 1.04 million ha, were estimated to be present in the Prairie Pothole Region of the Dakotas (Ruwaldt 1975; Stewart and Kantrud 1973; H.A. Kantrud, unpubl. data). The estimates were based on relatively small numbers of randomly sampled plots. Approximate basin numbers and areas by water regime were 698,000 temporary (113,000 ha), 1,474,000 seasonal (583,000 ha), and 127,000 semipermanent (345,000 ha). These basins were estimated to compose 84.8% of the area and 89.3% of the number of natural basins in the region; subsequent drainage and filling has further reduced the number of wetlands.

Distribution of these wetlands correlates with the distribution of various glacial landforms (for descriptions see Section 2.1). In both Dakotas, the greatest proportional area of semipermanent wetlands occurs in areas of dead-ice and terminal moraine, whereas the greatest proportional area of temporary and seasonal wetlands occurs in ground moraine and lake plain. The largest proportional area of semipermanent wetlands is found in the Missouri and Prairie Coteaus, whereas the less permanent wetlands are best represented in the Glaciated Plains and Lake Plains (Figure 3).

Density of basins can be $>40/km^2$ in some areas of dead-ice moraine or ground moraine, but the average is much less for the entire region, because some glacial and postglacial landforms contain few basins.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SCALE
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2 - Glaciated Plains
3 - Turtle Mountains
4 - Souris Lake Plain
5 - Devils Lake Plain
6 - Dakota Lake Plain
7 - Prairie Coteau

Figure 3. Major physiographic regions in the Prairie Pothole Region of the Dakotas.

CHAPTER 2. ABIOTIC ENVIRONMENT

2.1 GEOLOGY

Glaciation

About 7 million years ago, the subtropical climate of what is now the Dakotas began to change to a continental climate of cool winters and warm summers (Bluemle 1977). During the Pleistocene Epoch that followed, a succession of great ice sheets inched southward from Canada and covered most of the Dakotas (Figure 4). These huge glaciers transported vast quantities of rock and soil. Large amounts of local silty and clayey bedrock outcrops were also pulverized and added to the mixture, forming glacial drift or "till" that was deposited as sediment across most of the area glaciated. These deposits may be >250 m thick in places and are dotted with shallow basins left by the scouring or shearing action of the glaciers, or from the collapse of ice blocks left to melt in the deposits after the glaciers retreated. According to Flint (1955), many basins in South Dakota were formed when glacial drift materials blocked ancient bedrock valleys. Additional basins were formed by materials deposited by water flowing from melting glaciers. Thus, all the basin wetlands discussed in this report occur in a geologically young landscape.

The retreat of the glaciers is marked by the beginning of the Holocene Epoch about 10,000 years ago, as winters became cold and summers became hot (Bluemle 1977). The spruce-aspen forests of what are now the northern plains were succeeded by grasslands, and since that time, periods of warm, dry conditions have alternated with periods of cool, wet conditions. Some additional basins were formed during this period from wind-worked sand dunes, but nearly all of the basin wetlands in the Dakotas were formed as a direct result of glaciation or the melting of glacial ice. The area of depressional topography formed by a variety of geological processes comprises the famed Prairie Pothole Region, which, until the advent of European man, was an approximately 715,000-km^2 grassland-wetland complex that stretched from north-central Iowa to central Alberta. This region was unique because of its abundance of shallow-basin wetlands, which attracted most of North America's waterfowl during the breeding season.

Stewart and Kantrud (1973) estimated that 93% of the area and 94% of the number of wetlands in the Prairie Pothole Region of North Dakota were composed of natural basin wetlands, whereas the remainder were mostly streams and oxbows, stockponds and dugouts, reservoirs, road ditches and drainage channels, and minor types such as sewage lagoons. These figures show the importance of glaciation on the composition of wetlands in the region.

Physiographic Divisions

Geobotanists have traditionally divided the northern grasslands into

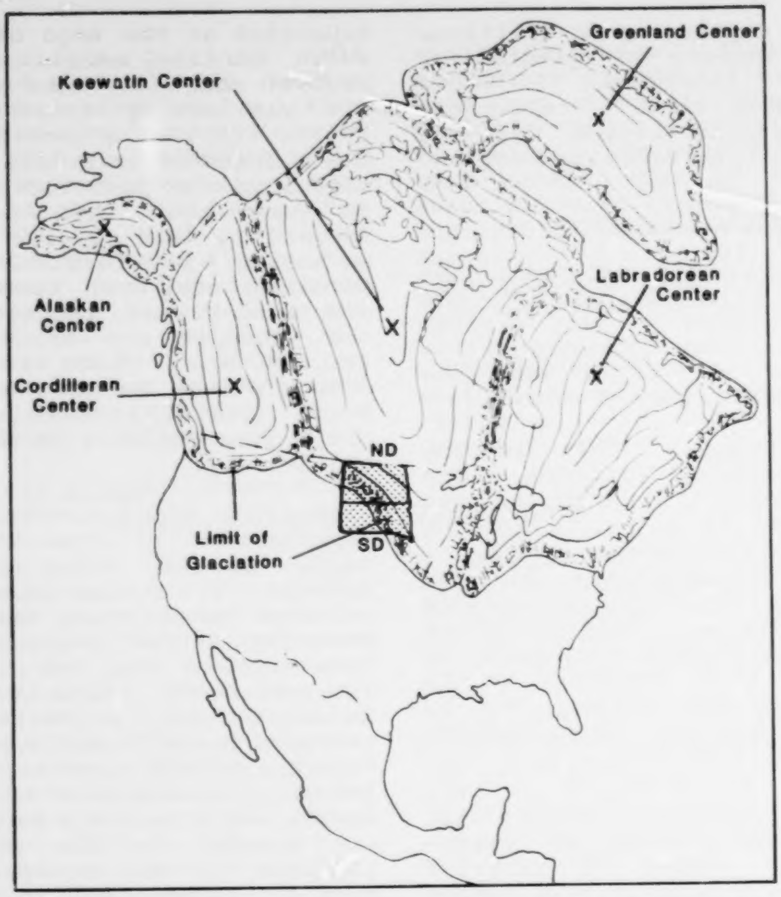


Figure 4. Extent of Pleistocene glaciation in North America in relation to North and South Dakota (modified from Bluemle 1977).

two large areas called the Great Plains and Central Lowland (Fenneman 1931) (Figure 1). The more arid Great Plains supports native grassland that is shorter than that in the moister Central Lowland to the east. The Prairie Pothole Region of the Dakotas encompasses portions of both these areas.

The Great Plains portion of the Prairie Pothole Region of the Dakotas contains a single physiographic division, the Missouri Coteau (Figure 3). This division is approximately 52,000 km^2 in area. The entire west slope of the Missouri Coteau drains to the Gulf of Mexico via the Missouri River.

By far the largest number and area of basin wetlands in the Dakotas occurs in the Central Lowland. Most of this land mass drains either to Hudson's Bay (North Dakota) or the Gulf of Mexico (South Dakota). Within the Central Lowland lie six major physiographic regions (Figure 3). These are, in decreasing order of area, the Glaciated Plains (91,000 km^2), Prairie Coteau (15,000 km^2), Dakota Lake Plain (5700 km^2), Souris Lake Plain (3600 km^2), Devil's Lake Plain (1400 km^2), and Turtle Mountains (1200 km^2).

All seven physiographic divisions contain a variety of glacial or postglacial landforms. Those landforms that contain relatively numerous wetland basins will be discussed in the following section.

Glacial Morainic Landforms

Most natural basin wetlands in the Prairie Pothole Region of the Dakotas are found in five glacial morainic landforms (Bluemle 1977). Moraine means any materials deposited directly by glaciers.

Ground moraine. This is the predominant glacial landform of the Glaciated Plains (Figure 3), and can be recognized by a gently rolling landscape with numerous shallow saucer-shaped depressions, but few hills or deep cup-shaped depressions (Bluemle 1977). This landform occurs where moderate amounts of glacial till were deposited at the base of a moving glacier and by collapse from within the glacier when it finally melted.

Washboard moraine. This form appears as small areas of irregularly spaced ridges of material thought to have been carried upward through the ice along shear planes parallel to the edge of the glacier (Bluemle 1977). Small basins are numerous in washboard moraine. This landform is mostly found in association with ground moraine in the Glaciated Plains.

Thrust moraine. This is perhaps the most spectacular glacial landform, as it is the result of large-scale glacial shearing that moved blocks of land up to 20 km^2 in area for short distances (Bluemle 1977). The "hole" left by these blocks commonly resulted in a large lake, whereas the hilly blocks often contain numerous small but relatively deep basins. Most thrust moraine is found in the Glaciated Plains.

Terminal moraine. This form resulted when glacial till was deposited at the edge of a glacier while the ice margin was melting back at about the same rate as the ice was moving forward (Bluemle 1977). Till is a general term for the mixture of materials ranging in size from clay particles to boulders of many tons that were pushed forward by and carried on top of advancing glaciers. Terminal moraines are most common in the Glaciated Plains, but also occur in the Missouri and Prairie Coteaus (Figure 3). These moraines are commonly 2-15 km wide and 5-90 km long. Basins in terminal moraine are highly variable in size, depth, and density.

Dead-ice moraine. This form is responsible for some of the most rugged glacial topography in the Dakotas; it formed when glaciers advanced over steep escarpments. Shearing action carried material into and on top of the glacier (Bluemle 1977). This insulated the underlying ice, which took several thousand years to melt and collapse. When the overlying materials slumped and slid, thousands of basins of all shapes and sizes were formed. Dead-ice moraine is the most common landform in the Missouri Coteau, Turtle Mountains, and Prairie Coteau. Smaller amounts of dead-ice moraine occur in the Glaciated Plains.

Glacial Meltwater Landforms

Three glacial meltwater landforms contain significant numbers of basin wetlands. These landforms were created by water from melted glacial ice, including precipitation on glaciers as they were melting (Bluemle 1977).

Glacial outwash plain. This form consists of sand and gravel that was deposited by water flowing from melting glaciers. In some of these broad plains are numerous large lakes, whereas in others are large numbers of very shallow depressions. This landform is mostly found in the Glaciated Plains.

Collapsed glacial outwash. This form resulted when glacial outwash was deposited on stagnant ice. When the ice melted, the sand and gravel slumped to form an irregular hilly surface with numerous wetlands, many of them large, shallow lakes (Bluemle 1977). Most collapsed glacial outwash occurs in the Missouri Coteau, but several large examples can also be found in the Glaciated Plains. Many of the largest basins in North Dakota are in collapsed glacial outwash, and many of the lakes formed in these basins are highly saline.

Glacial lake plains. These areas occur today where lakes of glacial meltwater stood for hundreds or thousands of years (Bluemle 1977). Glacial Lake Agassiz was the largest of such lakes in what now are the Dakotas. This giant water body once occupied a vast area encompassing most of southern Manitoba and Ontario, as well as huge areas of Saskatchewan and northern Minnesota. Nearly all the glacial lakes vanished when the glaciers receded and outlets were established. Topography is very flat in these areas, and wetland basins are very shallow. However, near the center of some glaciated lake plains, a few large remnant basins are still present. Most glacial lake plain in the pothole region occurs in the Dakota, Souris, and Devil's Lake Plains (Figure 3), but small areas also can be found in the Glaciated Plains and Missouri Coteau. In the latter area and the Turtle Mountains, there are also some small areas where glacial lakes flooded stagnant ice for shorter periods, resulting in hilly topography with numerous basins when the stagnant ice finally melted.

2.2 CLIMATE AND WEATHER

The Dakotas have a climate characterized by relatively short, moderately hot summers and relatively long, cold winters because these states lie in the middle of a large continent at middle latitudes. Temperature and precipitation data for Bismarck, ND, have been summarized for a 30-year period by Court (1974) and are shown in Table 2. This city lies at the west-central edge of the Prairie Pothole Region of the Dakotas. The continental nature of the climate is shown by the wide (85 °C) temperature extremes and relatively low (385 mm/yr) precipitation.

The following data on climate and weather have been summarized from Visher (1966), Black (1971) and Jensen (n.d.).

Temperature

Temperatures form roughly south-to-north gradients in the Prairie Pothole Region of the Dakotas. Normal annual temperature ranges from about 3 °C in northern North Dakota to about 8 °C in southern South Dakota. In January, the coldest month, temperatures average -19 °C in northeastern North Dakota and -8 °C in southeastern South Dakota. During July, the warmest month, the range is 16 °C to 23 °C for the two areas, respectively. Rapid plant growth begins when mean daily temperatures rise to 6.1 °C. The date for this event varies from about 26 April in northeastern North Dakota to about 3 April in southeastern South Dakota, a difference of over three weeks. Conversely, vegetative growth largely ceases when mean daily temperatures fall to 1.7 °C. This event occurs about 20 October in northern North Dakota and about 10 November in southeastern South Dakota. The normal length of the frost-free season varies from about 110 days in northern North Dakota to about 150 days in southeastern South Dakota. The frost-free season may be slightly shorter in basin wetlands, as cold air flows downhill and can accumulate in topographic depressions. Crops planted in and around wetlands often are the first to be injured by freezing temperatures, giving rise to what some farmers call "frost pockets."

Table 2. Climatic data for Bismarck, ND, 1931-60 (from Court 1974).

Month	Daily temperature (°C)			Mean precipitation (mm)	Mean snowfall (mm)
	mean	max.	min.		
Jan.	-12.8	12	-42	11	170
Feb.	-10.8	20	-37	11	150
Mar.	- 3.8	27	-35	20	220
Apr.	6.1	33	-19	31	70
May	13.0	37	- 7	50	20
June	18.1	38	1	86	tr.
July	22.3	42	4	56	0
Aug.	21.0	43	3	44	0
Sept.	14.8	41	- 9	30	10
Oct.	7.9	35	-15	22	40
Nov.	- 2.0	23	-28	15	140
Dec.	- 8.4	16	-38	9	130
Annual	5.4	43	-42	385	950

The highest summer temperatures officially recorded in North and South Dakota to 1945 were 49.4 °C and 48.9 °C, respectively, whereas the lowest official winter temperatures prior to 1952 (the last year for which summarized data are available) were -51.1 °C and -50 °C, respectively. Soils usually freeze to depths of 0.9-1.8 m in northern North Dakota and 0.5-0.9 m in southeastern South Dakota.

Winds and Storms

Surface winds average 21 km/hr in northeastern North Dakota and 17.7 km/hr in southeastern South Dakota. Meteorologists plot winds as net excesses of wind in a given direction during various time periods. For the region, there is a relatively large excess of wind from the northwest in January, and a relatively small excess of wind from the northeast in July. Many low-pressure cells track from west-northwest to east-southeast across the region during the year. The number of spring and summer thunderstorms ranges from 25 per year in northern North Dakota to 35 per year in southeastern South Dakota. This combination of temperature and wind differences cause the normal annual evaporation from pans to vary from 1.02 m in northeastern North Dakota to 1.65 m in southeastern South Dakota.

Precipitation

The relatively small amount of precipitation in the Canadian prairies has been attributed by Hare and Hay (1974) to the weakness of atmospheric disturbances and their associated uplift. Air masses move eastward from the Rocky Mountains and fall steadily toward lower elevations in the northern prairies. The rate of fall is sufficient to reduce cyclonic action appreciably, thus reducing the effectiveness of the mechanism that causes precipitation. This phenomenon also reduces precipitation in the Prairie Pothole Region of the Dakotas. The southern part of the region has more precipitation because it receives more moisture-laden airmasses from the Gulf of Mexico.

Annual precipitation in the region ranges from 33 cm in northwestern North Dakota to 58 cm in southeastern South Dakota. Larger amounts of spring and summer precipitation in the southeastern part of the region account for most of this difference. About 70% of the annual precipitation falls as rain during spring and summer, with June the wettest month. Distinctly dry years, having <75% of normal precipitation, occur with 10% frequency in northwestern North Dakota, but only 4% in southeastern South Dakota. There is a large gradient across the Prairie Pothole Region of the Dakotas in the length of the relatively dry season, that is, when weekly normals of <1.27 cm of precipitation can be expected. In northwestern North Dakota, this season averages 8-10 months, whereas in southeastern South Dakota, this season lasts only 2-5 months.

Snowfall in the region averages <1 m/yr, much less than areas directly to the east or west. In the dry northwestern corner of the region, 25% of normal annual precipitation falls as snow, whereas in southeastern South Dakota only 12% falls in this form. Appreciable amounts of snow fall on >60 days/yr in northeastern North Dakota, whereas significant amounts fall on only about 28 days/yr in southeastern South Dakota. Dry winters, when <7.6 cm of precipitation falls, occur one year in five.

Blizzards, as defined by the National Weather Service, are storms with wind speeds >51.5 km/hr, temperatures <-6.67 °C, and visibility not >152 m. Reduced visibility is caused by snow, blowing snow, or mixtures of snow and soil. North and South Dakota have a far greater frequency of blizzards than any of the adjacent states. North Dakota has 2.2 blizzards per year, with 54% of them originating as Alberta lows. South Dakota has 2.1 blizzards per year, with 52% of them originating as Colorado lows. Snow from February and March blizzards and snowstorms is often an important source of spring runoff for prairie wetlands.

Hail falls in moderate amounts compared to the rest of the nation, on an average of 2-4 days/yr. Brief heavy rains occur more frequently than in the arid west, but are only rare or occasional compared to the southeastern United States and the gulf coast. Normal annual water loss by runoff and evaporation is 0.36 m in northwestern North Dakota and 0.56 m in southeastern South Dakota; the rest enters the ground.

2.3 HYDROLOGY

Wetlands exist because specific geologic settings and hydrologic processes favor ponding of water or soil saturation. A unique combination of glaciation and climatic conditions in the Prairie Pothole Region has produced a large number of dynamic aquatic ecosystems that have a tendency to be nonintegrated (not receiving or contributing to channelized surface flow). Nonintegrated basins have the potential to impound large volumes of water and undergo long-term, rather extreme changes in water depth and biotic conditions in response to climatic trends. Water-level fluctuations in typical seasonal and semipermanent North Dakota wetlands are shown in Figure 5. Note the greater rate of water loss and greater frequency of dryness in the seasonal wetland. The low-grade shorelines of prairie wetlands combine with semiarid climate to produce dynamic wetlands; e.g., small increases in water level cause great increases in the proportion of a basin inundated, and conversely, hot, dry conditions often remove surface water from large areas of a basin in a relatively short time.

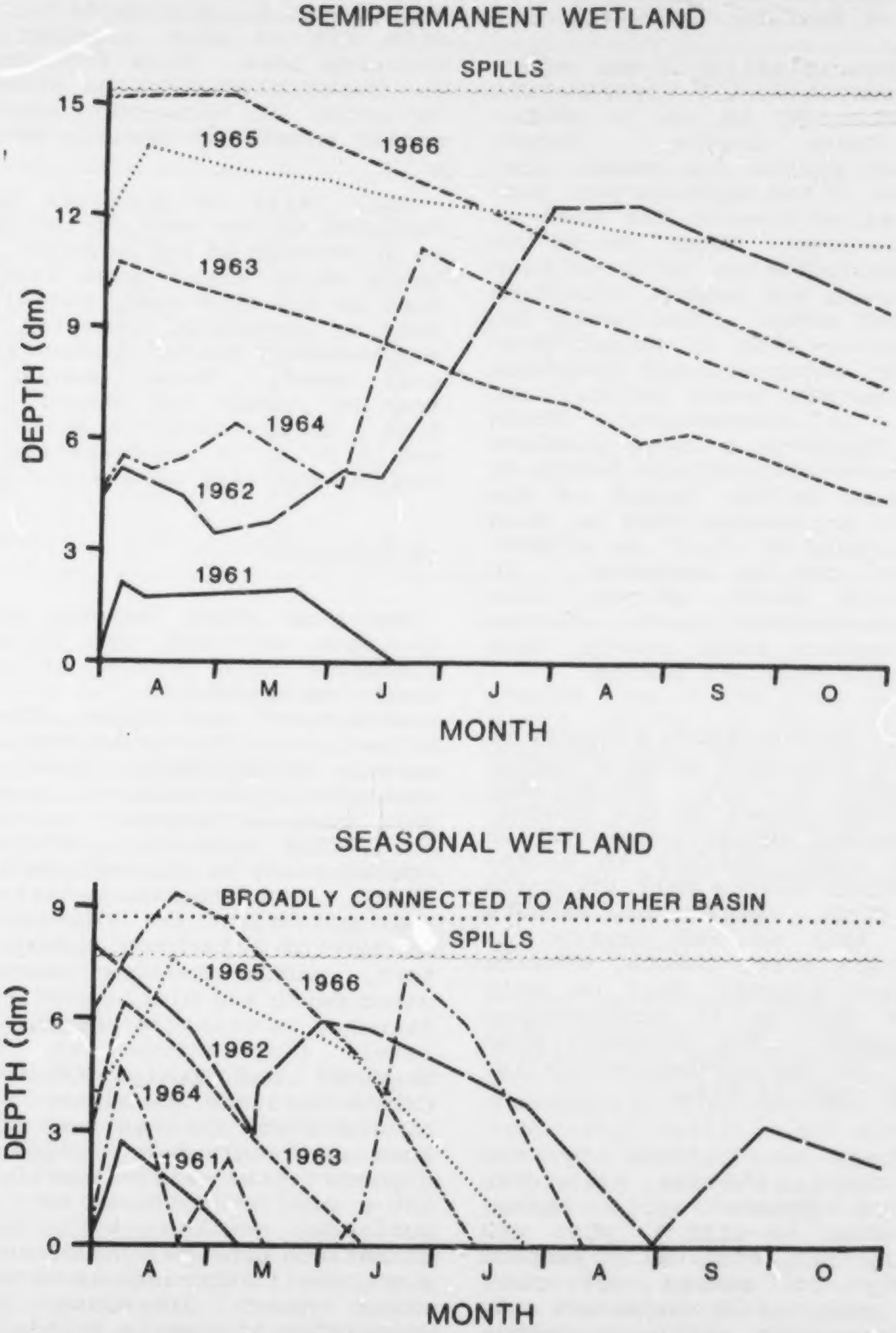


Figure 5. Water level changes during the ice-free season over a 6-year period in a seasonal (lower) and semipermanent (upper) basin wetland in North Dakota (from Kantrud et al. 1989).

Hydrologic regimes are dictated by climate and geology (Figure 6) that establish the environment for hydrologic processes (Winter 1989). Atmospheric, surface, and ground water interact with basin topographic setting and the hydraulic characteristics of glacial tills to establish wetland hydrologic functions. Precipitation and a combination of evaporation and transpiration are, respectively, the major components of water gain and loss in prairie wetlands (Winter and Woo, in press). Evaporation and transpiration are controlled largely by wind and vapor fluxes above the wetland. Areas like the Prairie Pothole Region with persistent winds, high summer temperatures, and dry overlying air masses can be expected to have high evaporation and transpiration rates during the summer months.

Lissey (1971) found that most of the water available for ground water recharge is derived from spring snowmelt. Snow collects in topographic depressions and 50% to 90%

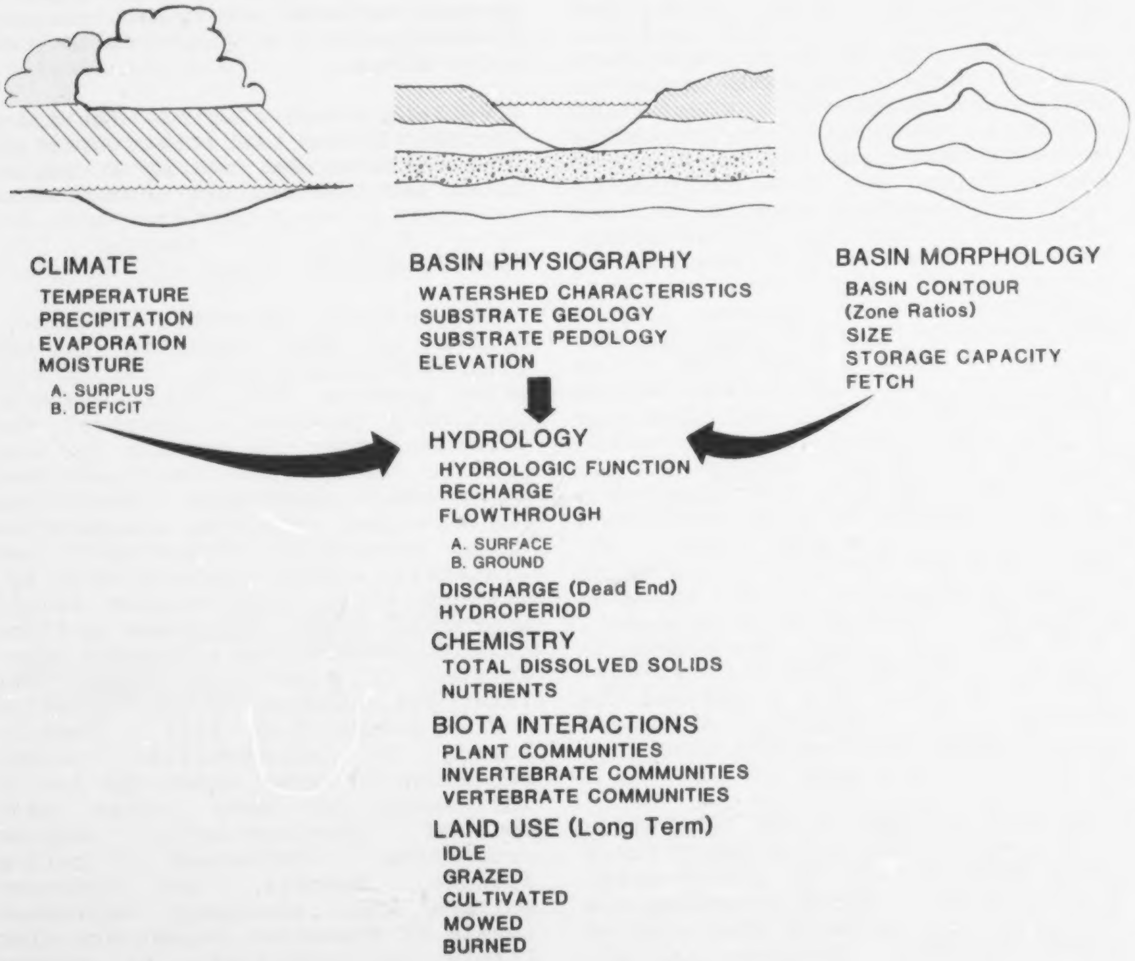

CLIMATE
TEMPERATURE
PRECIPITATION
EVAPORATION
MOISTURE
A. SURPLUS
B. DEFICIT
BASIN PHYSIOGRAPHY
WATERSHED CHARACTERISTICS
SUBSTRATE GEOLOGY
SUBSTRATE PEDOLOGY
ELEVATION
BASIN MORPHOLOGY
BASIN CONTOUR
(Zone Ratios)
SIZE
STORAGE CAPACITY
FETCH
HYDROLOGY
HYDROLOGIC FUNCTION
RECHARGE
FLOWTHROUGH
A. SURFACE
B. GROUND
DISCHARGE (Dead End)
HYDROPERIOD
CHEMISTRY
TOTAL DISSOLVED SOLIDS
NUTRIENTS
BIOTA INTERACTIONS
PLANT COMMUNITIES
INVERTEBRATE COMMUNITIES
VERTEBRATE COMMUNITIES
LAND USE (Long Term)
IDLE
GRAZED
CULTIVATED
MOWED
BURNED

Figure 6. Environmental factors influencing prairie wetland ecology.

of the meltwater from topographic highs collects in depressions because snow melts before the ground thaws. Lissey concluded that except for occasional intense storms, summer rainfall is not a major contributor to recharge in the uplands.

Glacial topography and geologically governed permeability variations have a significant effect on surface and ground-water hydrology. Tills in moraines are generally silty and clayey materials that are not very permeable. Outwash deposits, on the other hand, generally consist of stratified sand and gravel, materials that are very permeable. The tills in the eastern Dakotas tend to be much higher in shale-derived material. These tills are more clayey and less permeable to water than those to the west and south, which have a larger proportion of limestone, sandstone, and siltstone derivatives (Winter 1989). Because prairie wetlands are characteristically nonintegrated, ground-water flow systems play a dominant role in their hydrologies. Lissey (1971) described the principles of depression-focused ground-water recharge and discharge in the glaciated prairie of southwestern Manitoba. LaBaugh et al. (1987) studied the hydrology of a wetland complex in the Cottonwood Lake area of Stutsman County, ND, that contained wetlands situated at different altitudes along a topographic slope and hydraulic gradient. This area has been described in detail by Winter and Carr (1980). LaBaugh et al. (1987) confirmed the concept of depression-focused ground-water recharge and discharge as proposed by Lissey (1971).

Wetland basins in the Cottonwood Lake area perform three basic functions with respect to ground water (Lissey 1971). These functions are reflected in the water chemistry of these wetlands (Swanson et al. 1988). Some basins function as ground-water recharge areas; such basins tend to be temporarily or seasonally flooded; they hold water for only a few months each year, and the water is generally low in dissolved solids. Some basins are through-flow systems with respect to ground water; that is, ground water flows in through parts of their bed while other parts recharge ground water. Through-flow basins hold water over longer periods and the water tends to have higher concentrations of dissolved solids. Some basins serve only as discharge areas for ground water. Lakes that receive discharge from both regional and local ground-water flow systems and do not lose water to seepage or surface outflow are highly saline, having specific conductance as high as 70 mS/cm.

Wetland hydrologic functions control the chemical characteristics of prairie lakes, and as a result, plant and invertebrate communities.

2.4 WATER QUALITY

The shallow, eutrophic characteristics of most wetlands in the Prairie Pothole Region, coupled with warm summers and cold winters, routinely produce a chemical environment that is hostile to many aquatic vertebrates. Wetlands that experience anaerobic conditions during summer or winter are referred to as summerkill (Kling 1975) and winterkill lakes, respectively by, fishery biologists (Nickum 1970). Summerkill lakes, described by Kling (1975), produce high midsummer populations of planktonic algae that later die, causing oxygen depletion and a summer fish kill. Contributing to winterkills, oxygen depletion in water under the ice is influenced by snow cover that reduces photosynthetic oxygen production. Increases in carbon dioxide, ammonia, and hydrogen sulfide that accompany decreased levels of dissolved oxygen are also likely to contribute to stress caused by low oxygen. Total dissolved salts also increase in the open water under ice as its thickness increases because salts are driven out as water freezes.

The water balance of wetlands affects their structure and function because nutrient inputs and outputs are altered (LaBaugh 1986). Precipitation, surface runoff, and ground-water discharge are water sources that can contribute to the water and chemical budgets of wetland basins (Figure 7). Water losses occur through evaporation and transpiration, surface outflow, and ground-water recharge. The flow patterns that dominate a wetland basin dictate the hydrologic functions of the basin, water chemistry, and ultimately, the biota that will dominate the basin (Figures 8-10).

Atmospheric water tends to be low in dissolved salts, runoff tends to be intermediate, and ground water, depending on the characteristics of the substrate, tends to be high. The salt content of ground water reflects the solubility characteristics of till minerals (calcite, dolomite, and gypsum) and the distance the water travels along a ground-water flow path to the wetland. Ground-water flow can originate from local, intermediate, or regional flow systems. Local systems tend to be lower in dissolved salts, while regional systems in which the water travels a greater distance through till and perhaps bedrock tend to be higher in dissolved salts (Swanson et al. 1988).

The dominant salts carried by ground water are ultimately controlled by mineral composition and their solubility characteristics. Salts are dissolved and then redeposited as concentrations increase and more highly soluble salts are encountered. Once dissolved salts enter a wetland basin they can be concentrated by evaporation and transpiration or removed through surface outflow, ground-water recharge, or both. Undissolved salts can also be

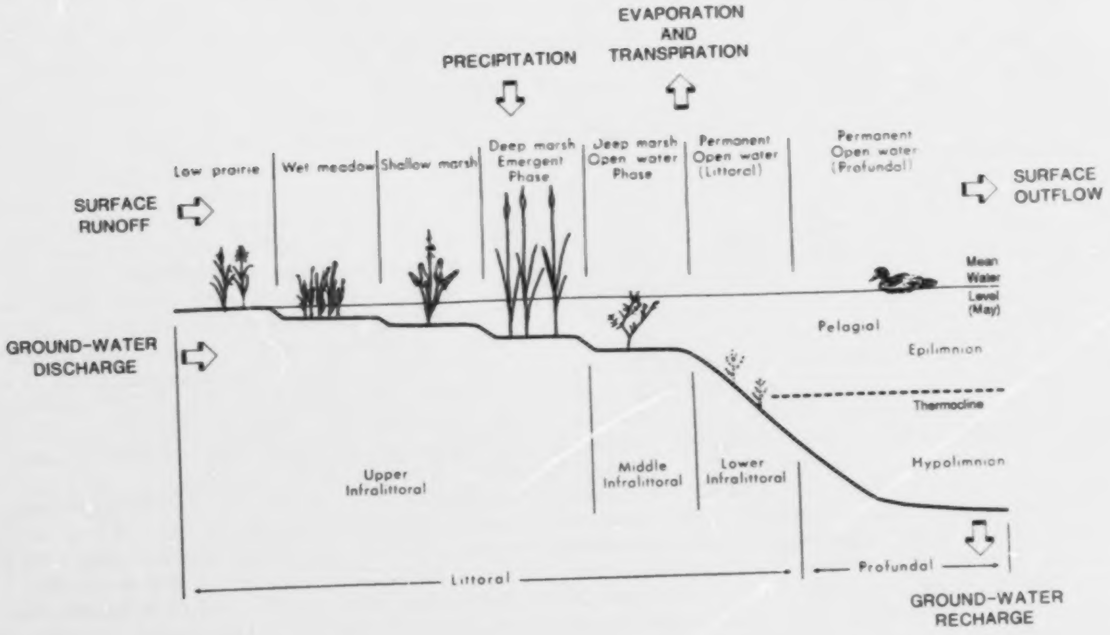

EVAPORATION
AND
TRANSPIRATION
PRECIPITATION
SURFACE RUNOFF
Low prairie
Wet meadow
Shallow marsh
Deep marsh Emergent Phase
Deep marsh Open water Phase
Permanent Open water (Littoral)
Permanent Open water (Profundal)
SURFACE OUTFLOW
Mean Water Level (May)
Pelagial
Epilimnion
Thermocline
Hypolimnion
GROUND-WATER DISCHARGE
Upper Infralittoral
Middle Infralittoral
Lower Infralittoral
Littoral
Profundal
GROUND-WATER RECHARGE

Figure 7. Dominant sources of water in prairie wetlands.

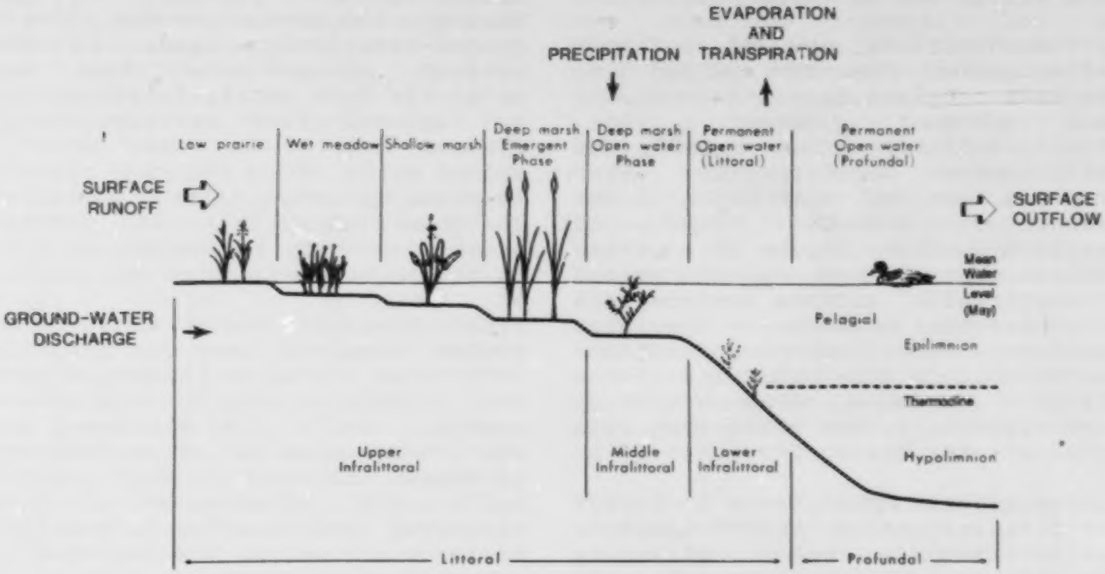

EVAPORATION AND TRANSPIRATION
PRECIPITATION
Low prairie
Wet meadow
Shallow marsh
Deep marsh Emergent Phase
Deep marsh Open water Phase
Permanent Open water (Littoral)
Permanent Open water (Profundal)
SURFACE RUNOFF
SURFACE OUTFLOW
Mean Water Level (May)
GROUND-WATER DISCHARGE
Pelagial
Epilimnion
Thermocline
Hypolimnion
Upper Infralittoral
Middle Infralittoral
Lower Infralittoral
Littoral
Profundal

Figure 8. Dominant flow pattern of a flow-through type of prairie wetland containing pooled water low in dissolved salts.

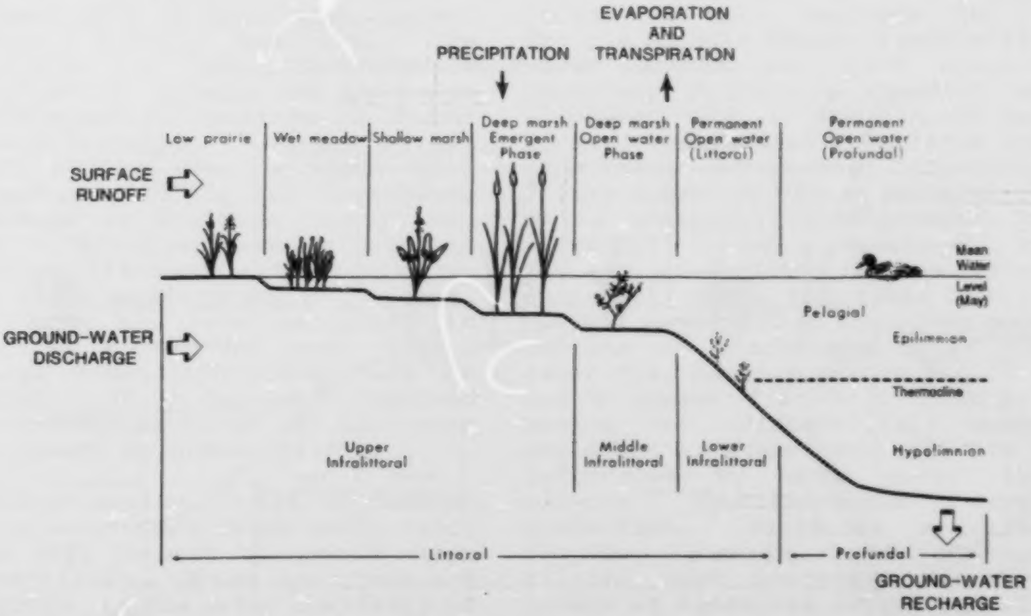

EVAPORATION AND TRANSPIRATION
PRECIPITATION
Low prairie
Wet meadow
Shallow marsh
Deep marsh Emergent Phase
Deep marsh Open water Phase
Permanent Open water (Littoral)
Permanent Open water (Profundal)
SURFACE RUNOFF
Mean Water Level (May)
GROUND-WATER DISCHARGE
Pelagial
Epilimnion
Thermocline
Hypolimnion
Upper Infralittoral
Middle Infralittoral
Lower Infralittoral
Littoral
Profundal
GROUND-WATER RECHARGE

Figure 9. Dominant flow pattern of a closed-system type of prairie wetland containing pooled water intermediate in dissolved salts.

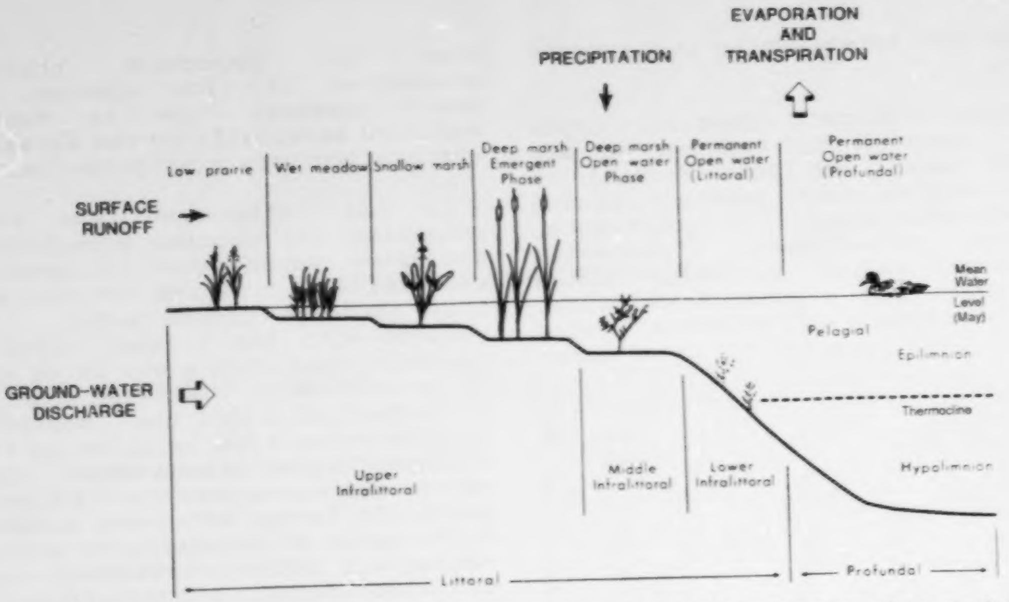

EVAPORATION AND TRANSPIRATION
PRECIPITATION
Low prairie
Wet meadow
Shallow marsh
Deep marsh Emergent Phase
Deep marsh Open water Phase
Permanent Open water (Littoral)
Permanent Open water (Profundal)
SURFACE RUNOFF
Mean Water Level (May)
Pelagial
Epilimnion
GROUND-WATER DISCHARGE
Thermocline
Hypolimnion
Upper Infralittoral
Middle Infralittoral
Lower Infralittoral
Littoral
Profundal

Figure 10. Dominant flow pattern of a hydrologic-sump type of prairie wetland containing pooled water that accumulates dissolved salts.

removed from dry basins or the dry shorelines of wet basins through wind erosion. Wetlands that lose water to surface outflow remove salts at rates that are a function of annual turnover rates (volume lost versus wetland storage capacity). As turnover rates increase, the salt content of the wetland approaches that of the dominant water source. Water loss to ground water also removes salts from the wetland. The rate of loss is influenced by the permeability of the till that controls the rate of export. Wetland basins that do not lose water to surface outflow, but are ground-water through-flow systems, tend, because of low permeability, to be higher in dissolved salts. Wetlands that lose water primarily to the atmosphere by evapotranspiration tend to concentrate salts to high levels (Swanson et al. 1988).

Wetlands differ from one another in their chemical characteristics based on their location in ground-water flow systems (LaBaugh 1989). Topography and the geologic characteristics of glacial tills provide the framework within which ground water flow systems develop.

Till in south-central North Dakota has a high percentage of silt and clay, is poorly sorted, and has low permeability; outwash is largely sand and gravel, is well sorted, and has high permeability (Swanson et al. 1988). Significantly higher average values of specific conductance and concentrations of sodium, potassium, sulfate, and alkalinity were found in wetlands located in outwash, whereas significantly higher average concentrations of calcium occurred in wetlands located in till (Swanson et al. 1988). Most wetlands that had values of specific conductance greater than 10 mS/cm in south-central North Dakota were located in outwash, and nearly all wetlands located in till had values less than 10 mS/cm. Saline wetlands located in outwash are topographically low, nonintegrated ground water discharge areas that function as hydrologic sumps and consequently concentrate salts.

Seven different chemical types were reported by Swanson et al. (1988) among wetlands studied in south-central North Dakota: calcium bicarbonate, magnesium bicarbonate, sodium bicarbonate, magnesium sulfate, sodium sulfate, sodium chloride, and magnesium chloride. The percentage of wetlands having the various chemical types of water were as follows: calcium bicarbonate-1, magnesium bicarbonate-22, magnesium sulfate-17, sodium bicarbonate-10, sodium sulfate-45, sodium chloride-4, and magnesium chloride-1 (Swanson et al. 1988). Specific conductivity of most of the wetlands (65%) was between 0.8 and <8 mS/cm. This range is within the oligosaline salinity category of the Cowardin et al. (1979) wetland classification system. Only 6% of the wetlands fell within the fresh category (<0.8 mS/cm). Twenty percent fell within the mesosaline category (8-<30 mS/cm), 7% were within the polysaline category (30-<45 mS/cm), 1% were within the eusaline category (45-60 mS/cm), and 1% were within the hypersaline category (>60 mS/cm) (Swanson et al. 1988).

A combination of hydrogeologic factors, including topography and geology, affect the water chemistry of wetlands (Driver and Peden 1977). LaBaugh et al.'s (1987) study of the Cottonwood Lake area, Stutsman County, ND, reveals that wetland chemistry is dependent on the position of individual wetlands with respect to ground-water flow systems. Ground-water flow systems integrate topography and geology that are important physical boundaries of flow systems. The basic chemical type is further modified seasonally by the excess of evaporation over precipitation.

In the Cottonwood Lake area, potassium and calcium bicarbonate-dominated waters low in specific conductivity occurred in wetlands that recharge ground water. The wetland with the largest value of specific conductance was in an area of ground-water discharge and was characterized by the magnesium sulfate water type, similar to that of the adjacent ground water. Concentration by evaporation is also an important factor affecting seasonal differences in chemistry of prairie wetlands. Different wetlands have different hydrologic relationships to ground water: some recharge groundwater, others discharge it, and still others do both.

Knowledge of the plant communities that occupy the different zones of a wetland basin (Stewart and Kantrud 1971) and the ionic composition of surface water can be used to draw inferences concerning the hydrologic functions of prairie wetlands (LaBaugh 1987; LaBaugh et al. 1987). Phosphorus and nitrogen differences were more closely related to the effect of hydroperiods on aquatic macrophytes (LaBaugh et al. 1987). The retention of phosphorus, nitrogen, and major ions by wetland basins is a function of their hydrologic settings as demonstrated in Figures 7-10 and described by Swanson et al. (1988). While phosphorus tends to be restricted to surface flow, nitrogen compounds that are water soluble can follow ground-water flow systems.

CHAPTER 3. BIOTIC ENVIRONMENT

3.1 PHYTOPLANKTON, PERIPHYTON, AND METAPHYTON

All algae, including wetland algae, are grouped according to the habitats they occupy. Floating algae are referred to as metaphyton. Algae suspended in the open water column or pelagic zone are referred to as planktonic algae (phytoplankton). Algae that grow attached to substrata and are a component of the periphyton (aufwuchs) are termed periphytic algae (Crumpton 1989). Periphytic algae can be further divided into those that grow within bottom sediments (epipelic algae), those that grow on plants (epiphytic algae), and those that grow on rocks (epilithic algae) (Crumpton 1989).

Aquatic macrophytes serve as a substrate for epiphytic algae. Thus seasonal changes in macrophyte abundance can influence the abundance and distribution of epiphytic algae as well as epipelic and epilithic algae that are often shaded by the macrophytes.

The role of algae in the primary production of prairie wetlands is not well defined (see Chapter 4).

Patterns of algal growth in seasonally flooded wetlands are influenced by hydroperiods and the apparent uptake and leaching of nitrogen and phosphorus associated with shallow marsh vegetation (LaBaugh et al. 1987). Wetland T8 in the Cottonwood Lake study area (Winter and Carr 1980) functions as a ground-water recharge area and dries up by midsummer (LaBaugh et al. 1987). Following snowmelt and flooding of dead shallow-marsh vegetation, dominated by Carex atherodes and Polygonum coccineum, decomposition begins. Shallow-marsh vegetation decomposes rapidly when flooded and releases nitrogen and phosphorus that are available for use by algae because this wetland has few submerged vascular plants competing with the algae for nutrients. When the water recedes, filamentous algae dominate the wetland surface until complete drawdown. New growth of shallow marsh vegetation and leaching of nutrients from the decomposing algae complete the cycle.

Semipermanently flooded wetlands also establish seasonal patterns of algal growth that tend to alternate with the growth of submerged vascular plants and periodic drawdowns. Wetland P11 in the Cottonwood Lake study area functions as a ground-water discharge area and is dominated by open water and beds of the submersed macrophyte Potamogeton pectinatus. During spring the shallow water in this wetland is turbid (Secchi disc depth=10 cm) and dominated by planktonic algae. As the summer progresses, epipelic and epiphytic algae and P. pectinatus stabilize the flocculent substrate and the water clears. During fall, when the P. pectinatus and benthic algae break down, the water again becomes turbid and planktonic algae dominate. Waterfowl contribute to the onset of turbid conditions by excavating the substrate in search of P. pectinatus turions.

Aquatic invertebrates, which are important foods of laying female dabbling ducks and their broods, tend to graze on periphyton or filter phytoplankton, bacteria, and organic detritus from the water column.

Phytoplankton species occupying a wetland complex in the Cottonwood Lake area of North Dakota are presented in Appendix A (LaBaugh and Swanson 1988). Wetland T8 is seasonally flooded and functions as a ground-water recharge area. Wetland T3 is seasonally flooded and functions as a through-flow system. Wetland P1 is a semipermanent wetland that does not have a surface outlet, but functions as a through-flow system with respect to ground water. Wetland P8 is a semipermanent wetland that contains a surface outlet and functions as a ground-water discharge area. Wetland P11 is a semipermanent wetland that does not have a surface outlet, functions as a ground-water discharge area, and concentrates salts through loss of water to the atmosphere.

Of the 306 taxa listed in Appendix A, 103 (34%) were Cyanophyta, 83 (27%) were Bacillariophyta, and 66 (22%) were Chlorophyta. Of the taxa 159 (52%) were found in seasonally flooded wetlands and 245 (80%) were found in semipermanently flooded wetlands. The more saline wetland P11 supported only 40% of the total taxa found on semipermanent wetlands, whereas the fresher wetlands P1 and P8 supported 81% (198 taxa).

3.2 MACROPHYTES

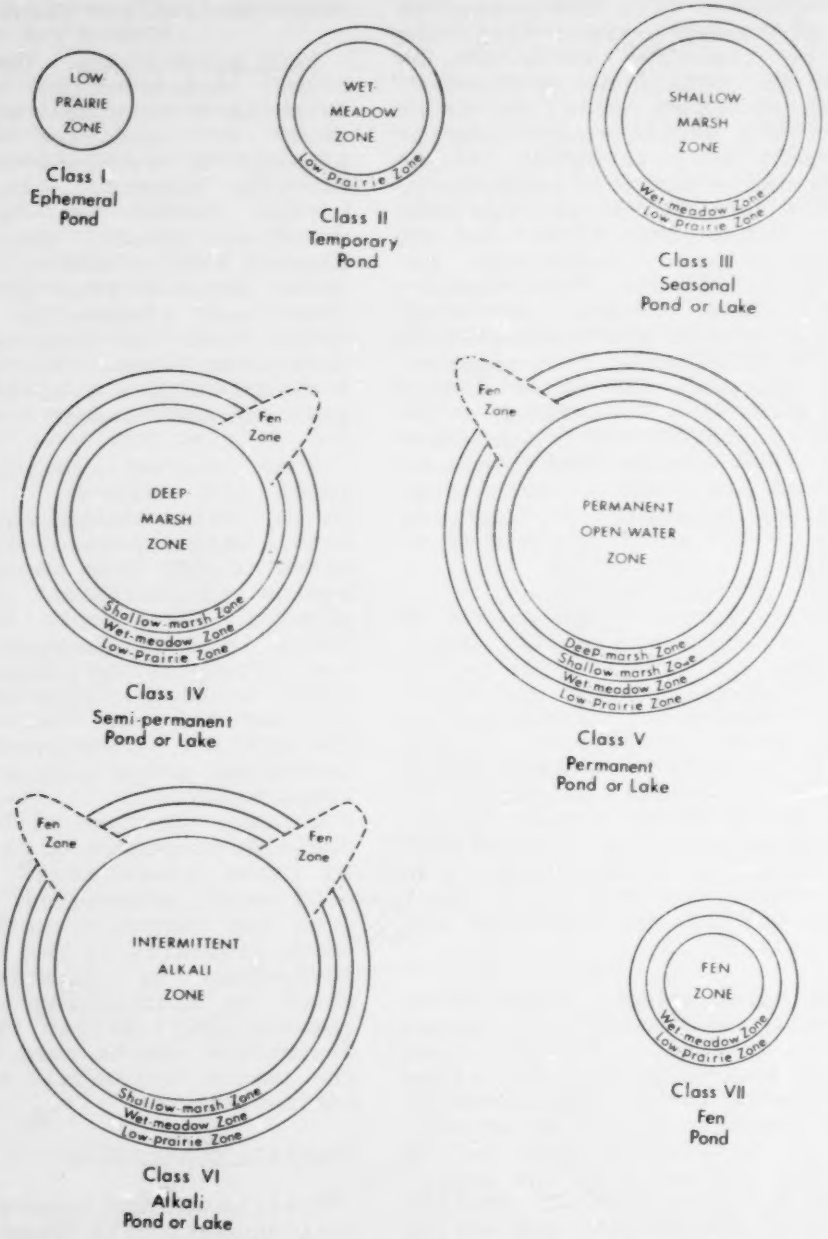
Information on the composition, structure, and classification of macrophytic vegetation of prairie wetlands has recently been reviewed by Kantrud et al. (1989). This paper also traces the history of wetland vegetation studies in the Prairie Pothole Region and discusses zonation, vegetation dynamics, and the major natural and human-related environmental factors that affect composition of hydrophyte communities in the region. Fire is considered a human-related disturbance and is included in this section, even though lightning-set (abiotic) fires commonly occurred on the prairies in pristine times (Higgins 1986). Lists of all hydrophytes found in North and South Dakota are found in Reed (1988a, b).

The early studies of Shunk (1917) and Metcalf (1931) identified the major features of prairie wetlands (central or concentric peripheral zones of vegetation) and the factors that seem to control plant species composition and distribution of these zones (water depth, length of time surface water or saturated soils are present, and salinity). Most subsequent investigations (e.g., Moyle 1945; Evans and Black 1956; Walker 1959, 1965; Dix and Smeins 1967; Smeins 1967; Walker and Coupland 1970; Stewart and Kantrud 1972; Barker and Fulton 1979; Kollman and Wali 1976) have elaborated on these themes and also described the effects of changes in water levels or salinity or the impacts of cultivation, grazing, fire, mowing, and idle conditions on wetland vegetation.

Zonation

Zonation of vegetation in prairie basin wetlands was first noticed by Froebel (1870) who described a "central portion" inside "concentric circles of different species of plants."

The vegetation of nearly all prairie basin wetlands is composed of a central zone bounded peripherally by concentric zones (Figure 11) that occupy the moisture-regime gradients (Figure 2). These zones are dominated by different species or groups of species. Changes in the size, color, or morphology of the species among zones makes them a prominent feature of the vegetation. The plants found in the zones are commonly grouped and accepted as indicators of the hydrologic regime


LOW PRAIRIE ZONE
WET-MEADOW ZONE
Low Prairie Zone
SHALLOW-MARSH ZONE
Wet-meadow Zone
Low Prairie Zone
Fen Zone
DEEP-MARSH ZONE
Shallow-marsh Zone
Wet-meadow Zone
Low-Prairie Zone
Fen Zone
PERMANENT OPEN WATER ZONE
Deep-marsh Zone
Shallow-marsh Zone
Wet-meadow Zone
Low Prairie Zone
Fen Zone
Fen Zone
INTERMITTENT ALKALI ZONE
Shallow-marsh Zone
Wet-meadow Zone
Low-prairie Zone
FEN ZONE
Wet-meadow Zone
Low Prairie Zone

Class I
Ephemeral
Pond

Class II
Temporary
Pond

Class III
Seasonal
Pond or Lake

Class IV
Semi-permanent
Pond or Lake

Class V
Permanent
Pond or Lake

Class VI
Alkali
Pond or Lake

Class VII
Fen
Pond

Figure 11. Spatial relation of vegetational zones in Stewart and Kantrud (1971) classes of natural basin wetlands in the glaciated prairies.

of the zones even though individual species have discrete distributions. The number of zones present in a basin increases with the degree of water permanency; that is, the length of time the zones can be expected to contain surface water. The best accepted names for these zones in the basins dealt with in this report are, in order of increasing degree of water permanency, wet meadow, shallow marsh, and deep marsh. Wet-meadow zones can be dominated by woody vegetation and not appear as meadow. The appearance of large amounts of woody vegetation around prairie wetlands is often attributed to fire suppression by European man (Bird 1961). Shallow-marsh and deep-marsh zones can be dominated by submersed plants. Wet-meadow and shallow-marsh zones are commonly cultivated and can be devoid of hydrophytes when dry or for short periods after reflooding.

Wet meadow zones. These zones of prairie wetlands are mostly dominated by low to medium-height grasses, rushes, sedges, and forbs or woody vegetation. Submersed or floating plants are absent. Inundation is usually temporary for a few weeks or months in spring or briefly after heavy summer rains. Water loss in centrally located wet-meadow zones in North Dakota can average >50 mm/day from early April till the end of May (Kantrud and Stewart 1977).

Shallow marsh zones. These zones are usually dominated by coarse emergent grasses, sedges, and burreed of midheight or a few, often nonpersistent, forbs. Submersed or floating vascular plants or aquatic mosses or liverworts are fairly common, and can occur in the understory of emergents or in shallow open water. Except for the spring snow-melt period, the presence of open water in shallow marsh zones is largely a function of land use. Inundation is normally seasonal from spring to mid- or late summer. Water loss in centrally located shallow-marsh zones in central North Dakota probably averages 40 mm/day from early April until the end of June (Kantrud and Stewart 1977).

Deep marsh zones. These zones are either dominated by tall, coarse cattails or bulrushes with an understory of submersed or floating plants, or by beds of submersed vascular plants. Unconsolidated bottom devoid of vegetation is sometimes found. Water regime is usually semipermanent, with surface water present from spring through fall and frequently overwinter. Water loss in centrally located deep-marsh zones in North Dakota wetlands likely averages 25 mm/day (Kantrud and Stewart 1977).

Some characteristics of these zones are evident. In a given basin, water depth increases with zonal water permanency, but this often is not true among or between basins of different hydrological setting. For example, shallow-marsh zones in many freshwater wetlands are often deeper than deep-marsh zones in more saline wetlands. In all but the most saline wetlands, the stature of emergent vegetation increases along the gradient from temporarily to semipermanently flooded. Species richness of the emergent component of the vegetation in these zones tends to decrease with water permanence. Deviations from the "normal" zonation pattern occur regularly in the form of zonal inversions or deletions brought about by fluctuating water levels (Smeins 1967; Millar 1976). Zonal deviations can be used to interpret the recent hydrologic history of a basin wetland.

Vegetation Dynamics

Prairie wetland vegetation changes more dramatically than most other natural vegetation in North America because of the effects of regional climatic instability on hydrologic regimes. Late winter snowfall, spring runoff, summer precipitation, and evapotranspiration are all highly variable between years and within seasons. Extended droughts as well as short series of years with much higher than average precipitation are common.

High water levels can kill up to 25% of the emergent vegetation in prairie wetlands, but when water levels fall, new bands of vegetation quickly develop on newly exposed shorelines (Walker 1959, 1965). Many emergent species such as Typha spp. reproduce vegetatively except during low-water conditions, when reproduction by seed is common (Bedish 1964). Extremely high water levels can also kill trees and other woody vegetation that have developed in wet meadow zones, leaving a ring of dead trees that can persist for years.

Stewart and Kantrud (1971) consider the degree of interspersion of cover and open water mostly a function of water depth rather than water permanency. Studies by Weller and Spatcher (1965), Weller and Fredrickson (1974) and van der Valk and Davis (1976, 1978a) on semipermanent Iowa wetlands outline the cyclic effects of physical and biological forces on the species composition and distribution of wetland vegetation.

The stages in this vegetation cycle are shown in Figure 12 and its effects on the biota are outlined in Table 3. In the dry-marsh stage, water is absent or low in the central zone and muskrats can be absent. Vegetation on the marsh floor consists of mudflat annuals

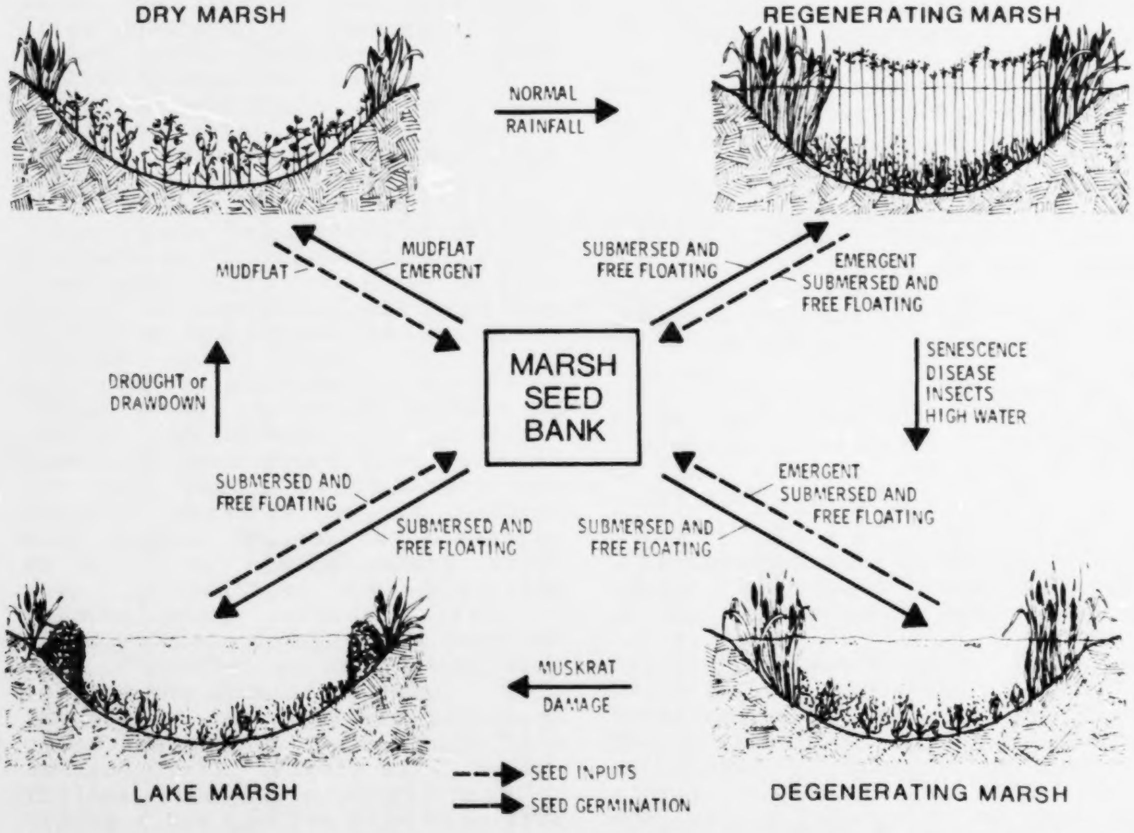

DRY MARSH
REGENERATING MARSH
NORMAL
RAINFALL
MUDFLAT
MUDFLAT
EMERGENT
SUBMERSED AND
FREE FLOATING
EMERGENT
SUBMERSED AND
FREE FLOATING
DROUGHT or
DRAWDOWN
MARSH
SEED
BANK
SENESCENCE
DISEASE
INSECTS
HIGH WATER
SUBMERSED AND
FREE FLOATING
SUBMERSED AND
FREE FLOATING
SUBMERSED AND
FREE FLOATING
EMERGENT
SUBMERSED AND
FREE FLOATING
MUSKRAT
DAMAGE
LAKE MARSH
DEGENERATING MARSH
SEED INPUTS
SEED GERMINATION

Figure 12. A generalized vegetation cycle in an Iowa prairie wetland (van der Valk and Davis 1978a).

Table 3. Stages of the typical habitat cycle in semipermanent Iowa wetlands (Weller and Spatcher 1965).

Stage name	Water in relation to basin capacity	Vegetation	Muskrat populations	Bird populations	Conspicuous indicator conditions
Dry marsh	Absent or low; emergents dry or nearly dry at base	Dense revegetation; most species find a suitable seedbed	Low to absent; populations centrally located	Red-winged blackbirds sparse; some use by upland birds	Red-winged blackbirds; few muskrat lodges; low water
Dense marsh; more vegetation than open water	Increasing water levels; emergents flooded	Very dense; rate of opening dependent upon muskrat populations and influence of flooding on certain species	Increasing	Numbers and variety increasing	Red-winged blackbirds increase; first yellow-headed blackbirds appear near sparse open pools; few coots and grebes
Hemi-marsh; open water and vegetation in about equal amounts	Median to near maximum	Muskrat eat-out; flotation and death; decline in shallow-water species; vegetative propagation	Increasing rapidly; well distributed	Maximum species diversity and production for most species	Many red-winged and yellow-headed blackbirds uniformly distributed; coot and pied-billed grebes abundant
Open marsh; more open water than vegetation	Maximum	Submergents and deep-water emergents persist; others absent or disappearing	Maximum or declining	Most species in decline; a few swimming species tolerate as long as long as some vegetation persist	Sparse bird populations and emergent vegetation
Open water marsh; virtually a eutrophic lake	Maximum or as low as median	*Scirpus acutus* may persist in sparse populations	Sparse; bank dens common	Red-winged blackbirds use shoreline vegetation; other species virtually absent	Red-winged blackbirds use shoreline shrubs and trees

and seedlings of emergent species. The annuals can complete their life cycle and add seeds to the seed bank during this stage. With the resumption of normal precipitation, the wetland enters the regenerating marsh stage. Muskrat populations begin to recover. Mudflat annuals decompose and are eliminated, but propagules of submersed and floating species from the seed bank germinate, and within a few years the emergent species spread vegetatively and normal patterns of zonation are established. Major inputs of seeds of the emergent species to the seed bank occur at this time. If water levels continue to rise, emergent vegetation begins to die from excess water depth, senescence, disease, and insects. This is the degenerating marsh stage. Continued high water results in the lake-marsh stage dominated by submersed vegetation only, because of excess muskrat damage and the inability of seeds of emergents to germinate under deep water. Finally, drought or artificial drawdown return the wetland to the dry-marsh stage.

The cycle described above for semipermanent wetlands in Iowa is idealized, and the role of the muskrat is more important there than in most of the pothole region of the Dakotas (see Section 3.7). Much more complex patterns of vegetation change occur in nature because of partial drawdowns or multiple drawdowns over short time periods. The less permanent temporary and seasonal wetlands do not undergo such complex cycles, but alternate on a wet-dry basis nearly every year. In addition, in the more arid Dakotas, water levels can fall so rapidly during drought that germination of mudflat annuals cannot keep up with the receding waters. This results in the drawdown bare-soil phase described by Stewart and Kantrud (1971) (Figure 13). Nevertheless, the rapid recruitment of plants a few species at a time from a much more species-rich seed bank seems to be a universal phenomenon related to the rapidly changing hydrological conditions of prairie wetlands.

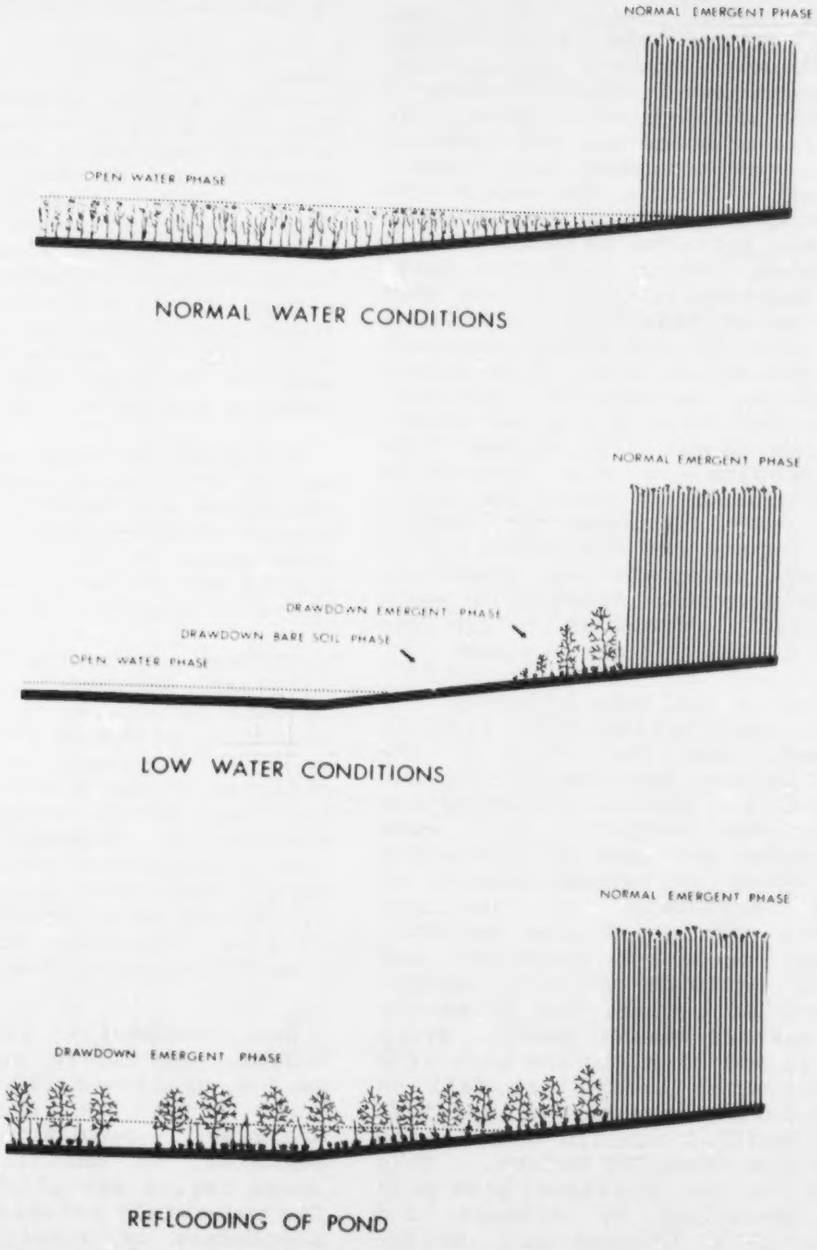
Effects of Water Quality

Much information has been gathered on the effects of salinity (concentration of total dissolved solids in the soil or water column) on prairie wetland vegetation since the early observations of Bailey (1888) and Visher (1912). Such information has been summarized recently by Kantrud et al. (1989). Areas containing large numbers of wetlands of relatively high salinity are mostly restricted to glacial outwash plains lying in the western and northwestern portion of the Prairie Pothole Region of the Dakotas.

The gradient from fresh to hypersaline water is a continuum, and any divisions are arbitrary. In this report we refer only to the salinity subclasses of Stewart and Kantrud (1971) and the water-chemistry modifiers of Cowardin et al. (1979).

Surface water in temporary and seasonal wetland basins in the Dakotas is usually fresh or slightly brackish, although a few moderately brackish seasonal basins have been observed (Stewart and Kantrud 1971). The fresh and slightly brackish subclasses of Stewart and Kantrud (1971) correspond to the fresh (<0.8 mS/cm) and lower oligosaline (0.8-2.0 mS/cm) water-chemistry modifiers of the Cowardin et al. (1979) classification system.

Semipermanently flooded wetland basins, and their associated wet-meadow, shallow-marsh and deep-marsh zones, can be fresh, slightly brackish, moderately brackish, brackish, or subsaline. Most of these basins are slightly brackish. The moderately brackish and brackish subclasses of Stewart and Kantrud (1971) correspond to the upper oligosaline (2.0-8.0 mS/cm) and lower mesosaline (8.0-15 mS/cm) modifiers of Cowardin et al. (1979), whereas the subsaline subclass


NORMAL EMERGENT PHASE
OPEN WATER PHASE
NORMAL EMERGENT PHASE
DRAWDOWN EMERGENT PHASE
DRAWDOWN BARE SOIL PHASE
OPEN WATER PHASE
NORMAL EMERGENT PHASE
DRAWDOWN EMERGENT PHASE

NORMAL WATER CONDITIONS

LOW WATER CONDITIONS

REFLOODING OF POND

Figure 13. A typical sequence of wetland phases as related to variable water conditions (Stewart and Kantrud 1971).

includes the range of the upper mesosaline (15-30 mS/cm) and polysaline (30-45 mS/cm) modifiers.

The general effect of increased salinity in any zone of wetland vegetation is to decrease the number of species. In polysaline wetlands, only the single submersed angiosperm Ruppia maritima occurs. A similar reduction in species is noted during drawdown conditions (Stewart and Kantrud 1971, 1972), when monodominant stands of Kochia scoparia are often found in dry polysaline basins. There also is a tendency towards succulence in plants found in more saline basins.

Salinity levels can fluctuate widely within and among seasons, particularly in smaller wetlands and those of intermediate and high salinity (Rozkowska and Rozkowski 1969, Stewart and Kantrud 1972). These changes can be accompanied by changes in vegetative species composition (Ungar et al. 1979). For example, aquatic bed dominated by Chara sp., Zannichellia palustris, and Potamogeton pectinatus often alternates with stands of Ruppia maritima in certain prairie wetlands as surface waters are respectively diluted and concentrated.

Common dominance types of emergent vegetation under various land uses and water chemistry conditions are shown for wetlands with temporary, seasonal, and semipermanent water regimes in Appendix B, along with similar information for the class aquatic bed.

It is difficult to establish meaningful salinity tolerances for individual species in their natural habitats, because of the complex of factors associated with salinity fluctuations and ecotypic variations among species (Kantrud et al. 1989). Nevertheless, we present the combined data of Smeins (1967), Disrud (1968), Sletten and Larson (1984), and H.A. Kantrud (unpubl.), as published in Kantrud et al. (1989) to estimate the salinity tolerance of many emergent and aquatic bed species in Appendix C. These are crude estimates because specific conductivities of surface waters and soil extracts from the root zone often differ greatly.

Many species have a broad range of salinity tolerance. This is a common trait among hydrophytes of the Prairie Pothole Region. Species that are tolerant of high salinities can survive low salinities (Ungar 1966). This suggests that competition or other factors play an important role in determining species composition in less saline sites (Ungar 1974).

Disturbance

Human-related disturbance is one of the most important factors affecting species composition of wetland vegetation in the northern prairies (Smeins 1967, Walker and Coupland 1968, 1970). The intensity of disturbance is often more important than the type of disturbance, and the native hydrophytes in the area are adapted to respond quickly to changing conditions and form dense stands. Common dominance types of wetland vegetation in various water regimes are related to disturbance and idle conditions in Appendix B.

Drainage and cultivation are the most extreme disturbances seen in most prairie wetlands in the Dakotas, although in some instances the basins themselves have also been destroyed by filling with earth or rocks, or used for solid-waste disposal (see Section 5.3).

Basins that are cultivated but not drained are extremely common in the Dakotas (Figure 14). Stewart and Kantrud (1973) estimated that 29% of the area and 52% of the individual wetlands in the Prairie Pothole Region of North Dakota had been cultivated for crop production in 1967, a year of excellent water

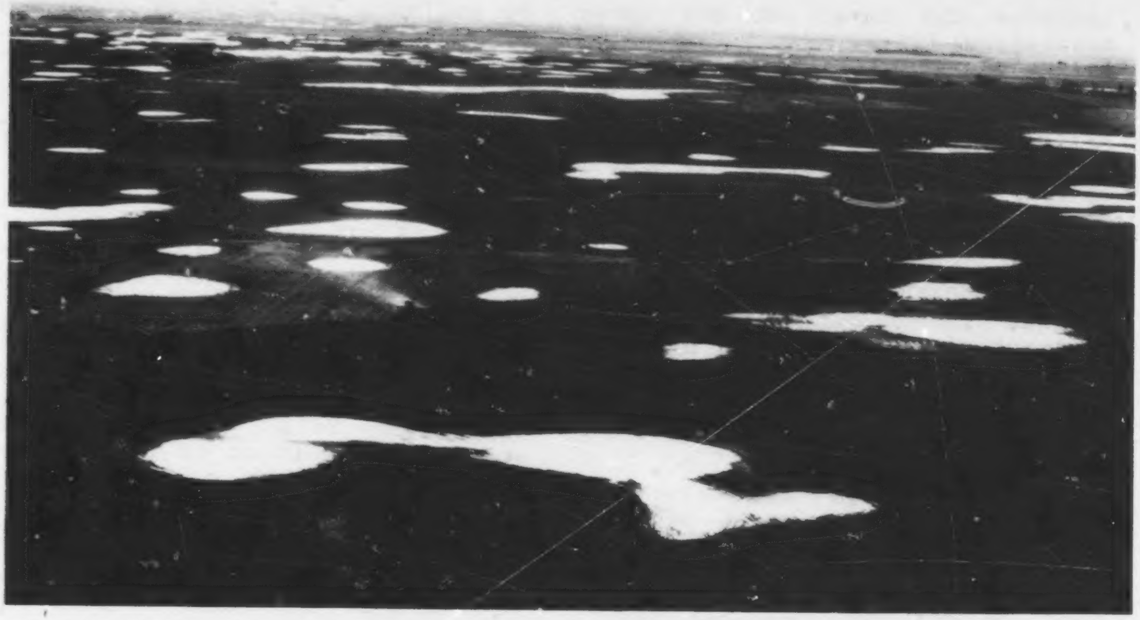


Figure 14. Cultivated temporarily and seasonally flooded basins dot the landscape in the intensively farmed regions of the Dakotas (near Lakota, North Dakota, June 1978; photograph by Alan Sargeant).

conditions. These wetlands were primarily temporary and seasonal. The wet-meadow and shallow-marsh zones of many semipermanent wetlands are also regularly cultivated. During the prolonged extreme drought of the 1930s, the bottoms of many basins with semipermanently flooded and intermittently exposed water regimes were used for crop production in the Dakotas. Sedimentation is extremely common in basins located in cropland in this area, as there is no barrier to runoff water from the uplands, and the practices of summer fallow and fall plowing are widespread. In addition, the heaviest rains of the season often occur just after seeding when fields are newly cultivated.

The main effect of cultivation on hydrophytic vegetation is to suppress or eliminate persistent emergent perennials and increase persistent and nonpersistent annuals. Aquatic-bed area also increases in cultivated shallow-marsh zones as canopies of emergents are opened and much easily colonizable unconsolidated shore is created.

Drawdown species invade cultivated basins very rapidly as water recedes, forming plant associations different from those found in similar basins in grassland. This is the cropland drawdown phase of Stewart and Kantrud (1971).

Basins cultivated intensively during dry periods often have no hydrophytic vegetation, or else the vegetation consists only of upland weeds, commercial crops, or their residue. This is the cropland tillage phase of Stewart and Kantrud (1971). Hydrophytes become reestablished from seed banks very quickly in these basins as water is replenished.

Another effect of cultivation is to roughen the bottom surface with ridges, furrows, clods, and wheel tracks. This creates a variety of microhabitats in which field weeds as well as emergent and submersed hydrophytes and drawdown species live in close proximity or patterned stands.

Prairie wetlands evolved under a regime of grazing by native ungulates; grazing by domestic livestock today remains as one of the most important commercial uses of these basins. Many basins located near feedlots or corrals around ranches or farmsteads are grazed all year, whereas those in outlying pastures are usually grazed during spring, summer, and fall. In pastures where artificial watering facilities are not provided and basins are few, basin wetlands can receive an inordinate amount of trampling and grazing pressure. Cattle are the most frequent grazers of Dakota wetlands, but sheep and horses are not uncommon.

Dominant plant species in grazed prairie wetlands usually differ greatly from those in areas put to other uses (Kantrud et al. 1989). Adaptations of wetland plants to grazing include nodal rooting and unpalatability (Walker and Coupland 1968). Unless unusually severe, grazing of wetlands results in greater species diversity, more complex distributional patterns, and sharper boundaries between zones (Bakker and Ruyter 1981). General effects of moderate to heavy grazing in prairie wetlands also include a decrease in overall height of emergents and an increase in aquatic bed. Schultz (1987) showed that prescribed grazing of monodominant Typha glauca stands by cattle in South Dakota wetlands resulted in a decrease in live stems, dead stems, depth of residual litter, and litter coverage. Associated changes included increased coverage of floating plants (Lemna and Riccia), higher water temperature, greater invertebrate abundance and biomass, and increased use by breeding waterfowl. Livestock trampling can affect the height and density of wetland vegetation more than consumption (Hilliard 1974). Severe grazing can decrease primary production (Reimold et al. 1975), increase water turbidity (Logan 1975), and eliminate all vascular plants (Bassett 1980).

Plants that are increased by or are tolerant of domestic livestock grazing in wetlands in or near the Prairie Pothole Region have been listed by Evans et al. (1952), Smith (1953), Smeins (1965), Dix and Smeins (1967), Walker and Coupland (1968), Stewart and Kantrud (1972) and Millar (1973). The relation of grazing to wetland vegetation and the use of such habitats by breeding waterfowl and their broods has been reviewed by Kantrud (1986a).

Removal of perennial emergent vegetation for use as livestock food or bedding is a common practice in the Prairie Pothole Region. Mowing is usually restricted to temporary and seasonal wetland basins and the wet-meadow and shallow-marsh zones of semipermanent wetlands, but during droughts even the coarse emergent species of deep-marsh zones are sometimes harvested. Wetlands thus treated appear as open water after spring runoff, but regrowth of emergents is rapid except under extremely high water levels, so by late spring a dense canopy of vegetation is usually present. Smeins (1967), Walker and Coupland (1968, 1970), and Stewart and Kantrud (1972) suggested that certain native hydrophytes were favored by mowing. However, J.B. Millar (unpubl. data, Canadian Wildlife Service) saw no detectable changes in the dominant emergent species in Saskatchewan wetlands after 25 years of mowing. Two introduced species, Alopecurus arundinacea and Phalaris arundinacea, are often planted in prairie wetlands for use as hay or forage crops.

Burning is not a common practice on privately owned wetlands in the Dakotas. A small proportion of the basins are burned each fall incidental to burning road rights-of-way for snow control; other basins are burned to make fall tillage easier or to decrease the amount of snow trapped in them so they can be more easily cultivated the following spring. Burning is being increasingly employed as a means to control excessive emergent vegetation to increase waterfowl production on National Wildlife Refuges and state-owned lands, yet little is known about the environmental effects of fire in prairie wetlands, and research on prescribed burning for wildlife production has often been urged (Ward 1968; Weller 1978; Kantrud 1986a).

Fires were common in prairie wetland vegetation in the early 19th century, as evidenced by the accounts of early traders and travelers. For example, in 1803 Henry and Thompson (Coves 1965) recorded fire rushing through "low places covered with reeds and rushes." In 1858 or 1859 Boller (1972) saw a large conflagration spread for many miles after being set by American Indians in "dry rushes in the prairie bottoms." Denig (1961), writing about his experiences during 1833-54, noted that fire would sweep over ice through wetland vegetation.

General references (Kozlowski and Ahlgren 1974; Wright and Bailey 1982) indicate that burning of marsh vegetation releases nutrients, opens the canopy and detrital layer, and allows for increased insolation and resultant earlier warming of bottom soils. Biological productivity usually increases following fire, even though plant species composition can be altered. Species composition usually changes little when perennial species with meristems at or below ground level are burned during their dormant period.

The few studies and incidental observations of fire effects on prairie wetlands (reviewed in Kantrud 1986a) do not currently provide wetland managers with sufficient quantitative information to formulate burn prescriptions. Most experimental burns, often in combination with crushing, mowing, water level manipulations, or herbicide trials, have been directed toward control of cattails (Typha spp.).

Many prairie wetland basins now lie idle in former pastures converted to cropland or in retired cropland or wildlife management areas. Even many of the larger semipermanent wetlands are not used for grazing because in recent decades livestock numbers have generally decreased in the eastern Dakotas. In addition, the dense stands of coarse emergents, particularly Typha spp., that have developed in these basins are relatively unattractive to livestock.

Biologists have often attributed decreased use of prairie wetlands by aquatic birds to decreased habitat heterogeneity caused by a reduction in the natural ecological processes of grazing, fire, and water-level fluctuations. In the absence of such processes, autogenic succession tends to build dense stands of emergent hydrophytes in many wetlands (Walker 1959; Jahn and Moyle 1964; Whitman 1976). In the prairies, the usual result is domination by tall robust grasses, sedges, cattails, or woody plants (Kantrud 1986a).

All but the more saline or steep-sided prairie wetland basins are susceptible to the establishment of dense stands of emergents because of low-gradient shorelines, small differences in soils or organic-matter content within basins, and the ability of many species to survive under a wide range of water conditions (Hammond 1961, Walker and Coupland 1968). Dense emergents can be controlled by water-level manipulation, but few natural basins in the prairie region have water-control structures or sufficient depth below natural spill elevation to make such structures effective if installed.

Drastic environmental changes occur when deep-marsh zones are allowed to go idle and stands of tall emergent hydrophytes become dominant. Reduced insolation of the water column and bottom substrate and increases in litter can reduce or eliminate other species of plants in the understory (Bennett 1938; Buttery and Lambert 1965; Spence and Chrystal 1970; Vogl 1973). Submerged plants, in particular, require water of sufficient depth to reproduce (Anderson 1978; Courcelles and Bedard 1978), and the buildup of litter and organic material from emergent species can reduce water depth or eliminate shallow-water areas (Ward 1942, 1968; Walker 1959; Hammond 1961; Beule 1979).

Buildup of litter and its shading effect also can result in lower soil or water temperature and lower rates of plant decomposition (Willson 1966; Godshalk and Wetzel 1978). Various emergent species can decompose at different rates as the result of differences in species composition of macroinvertebrate populations (Danell and Sjoberg 1979). Thus, the development of monotypic stands of emergents can effectively remove some of the variation in decomposer organisms that could act to maintain or increase vegetative heterogeneity.

Species Composition and Abundance

Common dominance types of emergent wetland vegetation are shown for temporarily, seasonally, and semipermanently flooded moisture regimes in Appendix B. Dominance types in aquatic bed in seasonally and semipermanently flooded moisture regimes are shown in Appendix C. These tables also relate species composition to land use and water chemistry. Additional species, mostly of lesser importance as vegetative cover, are listed in Stewart and Kantrud (1971, 1972).

3.3 INVERTEBRATES

Characteristic groups of wetland invertebrates can be associated with four major habitat types. These groups include benthic invertebrates that live in mud or in association with the mud-water interface, pelagic invertebrates that occupy the water column, macrophyte-associated invertebrates that live in or on vascular plants in association with periphyton communities, and neustonic invertebrates that live on the surface film. Some species occupy several habitat types during different phases of their life history. Schultz (1987) showed that livestock grazing of monodominant Typha stands in semipermanently flooded South Dakota wetlands resulted in increased invertebrate abundance and biomass, especially forms adapted to detritivory.

Herbivores and detritivores that live on wetland substrates feed on fallout from the water column and epipelic algae. Those that occupy the water column consume plankton and suspended organic particulates. Plant-associated invertebrates feed mostly on periphyton. Macroinvertebrates that live on the water surface (neuston) are primarily predators or scavengers.

Prairie-wetland invertebrate-species structure is controlled by basin hydrologic functions and associated chemical characteristics. The length of time between spring flooding and summer drawdown determines what fauna can occupy a given wetland basin. Temporarily and seasonally flooded wetlands are dominated by invertebrates that can complete their life cycles before the basins dry out. Invertebrates that neither fly, tolerate extended periods of desiccation, nor produce eggs that tolerate desiccation are eliminated during drought, and require some form of dissemination to facilitate their reintroduction into nonintegrated isolated wetlands (Swanson 1984). Transport mechanisms involved in reintroduction are important to our understanding of the ecology of wetland complexes in the Prairie Pothole Region (Swanson 1984).

Basin morphology, as well as hydrologic function and water quality, influences the fauna that will occupy a prairie wetland Swanson et al. 1984). Wetland P1 of the Cottonwood Lake area (Swanson 1987a) contains a large, shallow bay dominated by wet meadow and shallow marsh (Figure 15). This wetland (foreground, Figure 16) has no surface outlet, and as a result, responds to surface runoff by flooding and maintaining a large shallow-marsh zone nearly every spring. The invertebrate fauna of this zone is typical of the many isolated seasonally flooded basins in the area. Wetland P8 (background, left, Figure 16) is located in a valley of high relief and also contains a surface outlet (Figure 17). As a result, water levels are stable, and this wetland is dominated by open water and a deep-marsh zone and supports a fauna similar to the deep-marsh zone of wetland P1. The stable water and abruptly sloping shoreline greatly restrict the wet-meadow and shallow-marsh zones and their associated fauna.

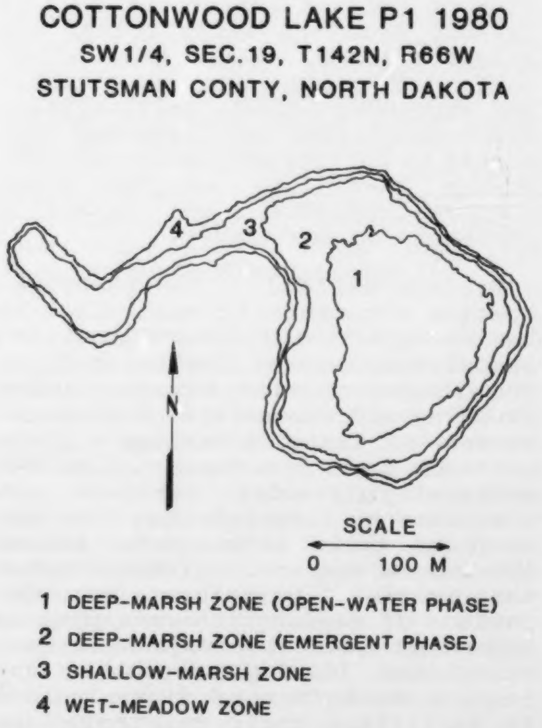

COTTONWOOD LAKE P1 1980
SW1/4, SEC.19, T142N, R66W
STUTSMAN CONTY, NORTH DAKOTA
4
3
2
1
N
SCALE
0
100 M
1 DEEP-MARSH ZONE (OPEN-WATER PHASE)
2 DEEP-MARSH ZONE (EMERGENT PHASE)
3 SHALLOW-MARSH ZONE
4 WET-MEADOW ZONE

Figure 15. Wetland P1 of the Cottonwood Lake, ND, study area showing vegetative zones.

Because water loss in many prairie wetlands is dominated by evapotranspiration rather than surface outflow or ground-water recharge, dissolved salts concentrate and influence the invertebrate fauna. As salt concentrations increase, the fauna is eventually dominated by salt-resistant species such as brine shrimp (Artemia salina) and shore flies (Ephydra spp.) (Swanson et al. 1988).

The invertebrate taxa associated with prairie wetlands are typical of the many taxa described for eutrophic and alkaline lakes and temporary and vernal ponds of the United States by Pennak (1978). There is little work, however, on the systematics of aquatic invertebrates that occupy the different wetland classes in the Prairie Pothole Region of North America (Murkin 1989). Some exceptions are the aquatic mollusk (Clarke 1973, 1981; Cvancara 1983), zooplankton (LaBaugh and Swanson 1988), and the aquatic Coleoptera (Hanson and Swanson 1989). Macroinvertebrates associated with semipermanently, seasonally, and temporarily flooded basins have been described in feeding-ecology studies of breeding waterfowl summarized by Swanson and Duebbert (1988). Schultz (1987) described the invertebrate taxa of semipermanently flooded basins in Day County, SD, during the summers of 1984 and 1985.

The aquatic mollusks of North Dakota consist of 44 species, of which 13 are mussels, 9 are pill clams, and 22 are snails (Cvancara 1983). Snails, however, account for a major segment of the fauna of

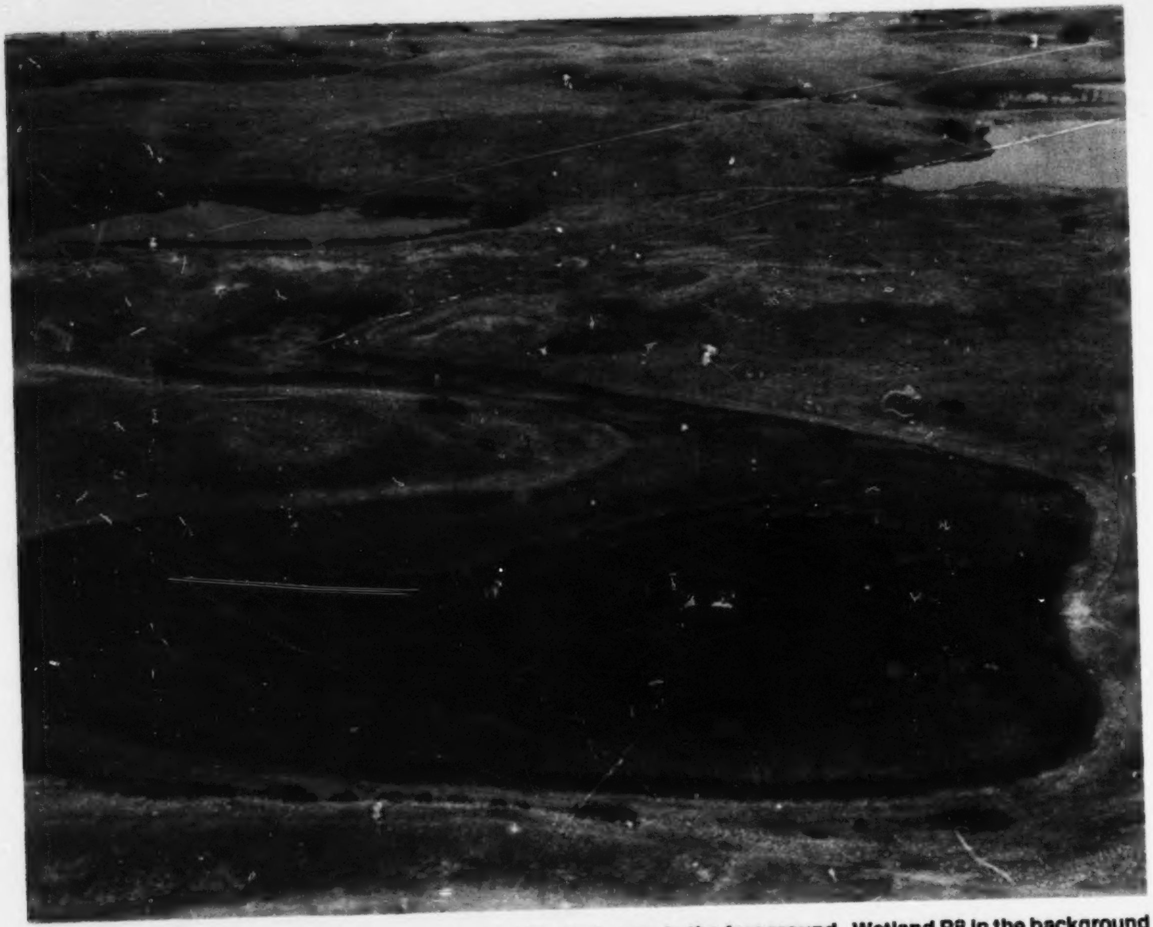


Figure 16. Wetland P1 of the Cottonwood Lake, ND, study area in the foreground. Wetland P8 in the background to the left.

seasonally and semipermanently flooded prairie wetlands. Twenty-one species of snails have been identified in the Hudson Bay drainage of North Dakota and eighteen species in the Mississippi River drainage. Mussels and most pill clams are confined to flowing water and permanent lakes.

The distribution of snails in prairie wetlands is influenced by hydroperiod and salinity. Molluskan species associations described by Cvancara (1983) for North Dakota are controlled by wetland hydrologic functions. Each wetland contains several wetland zones (Stewart and Kantrud 1971) that are determined by interactions between basin hydrologic functions and basin morphology. Large shallow-marsh zones of semipermanently flooded wetlands contain invertebrate species that are similar to those found in isolated seasonally flooded basins. Climatic conditions cycle wetland basins between extremes of flooding and drawdown that alter zones and their associated invertebrate fauna (Swanson 1987b).

Aplexa hypnorum-*Gyraulus circumstriatus* associations are found in

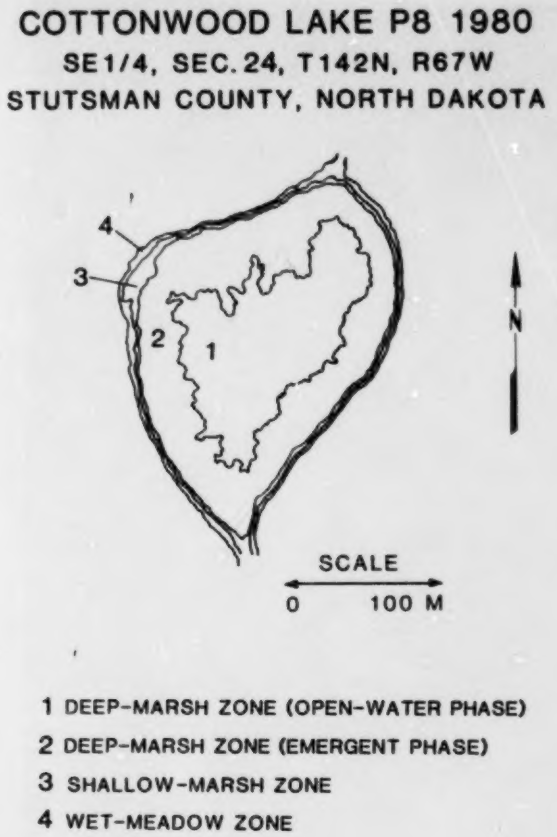

COTTONWOOD LAKE P8 1980
SE1/4, SEC.24, T142N, R67W
STUTSMAN COUNTY, NORTH DAKOTA
4
3
2
1
N
SCALE
0
100 M
1 DEEP-MARSH ZONE (OPEN-WATER PHASE)
2 DEEP-MARSH ZONE (EMERGENT PHASE)
3 SHALLOW-MARSH ZONE
4 WET-MEADOW ZONE

Figure 17. Wetland P8 of the Cottonwood Lake, ND, study area showing vegetative zones.

seasonally flooded basins or seasonally flooded zones of semipermanently flooded basins. Other molluskan species found in this association include *Promenetus umbilicatellus*, *Armiger crista*, *Stagnicola caperata*, *Physa jennessi*, *Promenetus exacuous*, and *Pisidium casertanum* (Cvancara 1983).

Helisoma trivolvis-*Lymnaea stagnalis* associations are found in permanent and semipermanently flooded lakes. Molluskan species that are part of this association include *Cincinnatia cincinnatiensis*, *Amnicola limosa*, *Pisidium nitidum*, *Valvata tricarinata*, *Helisoma anceps*, *Physa gyrina*, *Gyraulus parvus*, and *Stagnicola elodes* (Cvancara 1983). The first five species are found primarily in permanent lakes. However, permanent lakes that contain large semipermanently and seasonally flooded zones will contain molluskan species that are associated with these zones.

Wetland basins dominated by deep-marsh and shallow-marsh zones support pulmonate snails that produce relatively thin shells and do not have gills. Members of this subclass can occupy habitats that routinely exhibit anaerobic conditions. They respond to low dissolved oxygen by moving to the surface where they can use atmospheric oxygen. Factors influencing gastropod distribution include water permanency, total dissolved salts, dissolved oxygen, and substrate characteristics. Waters with >20 mS/cm conductivity do not support mollusks. Some species, however, such as *Stagnicola elodes*, *Physa jennessi*, and *Armiger crista*, tend to tolerate elevated concentrations of dissolved salts (Cvancara 1983). Mollusks occupy spring seeps associated with saline lakes (Swanson et al. 1984). Mollusk scientific names used in this report follow those used by Clarke (1981). Aquatic mollusks play an important role in the food web of prairie wetlands (Cvancara 1983; Swanson et al. 1974; Pennak 1978).

Crustaceans are a major component of the invertebrate fauna of prairie wetland complexes. Species structure within a wetland complex is influenced by hydroperiod and salinity. Two species of amphipods, *Gammarus lacustris* and *Hyalella azteca*, dominate the macrocrustacea of semipermanently flooded wetlands. The former species occupies wetlands that have an extended wet phase, are low in dissolved salts, and have relatively deep, cool water. *Hyallela azteca* occupies most semipermanently flooded wetlands. Both species routinely invade seasonally flooded wetlands by attaching themselves to aquatic birds and mammals during the summer months, but are eliminated during drawdown (Swanson 1984). Amphipods are replaced by salt-tolerant Anostraca as salt concentrations increase (Swanson et al. 1984).

Decapods are not found in nonintegrated wetland basins in south-central North Dakota, but are found in oxbow lakes and integrated wetlands in the headwater areas of tributaries that feed perennial river systems.

Eubranchiopods, such as Anostraca (fairy shrimp), Conchostraca (clam shrimp), and Notostraca (tadpole shrimp), are the dominant macrocrustaceans occupying temporarily and seasonally flooded basins in the Prairie Pothole Region. Fairy shrimp are also found in large wet-meadow and shallow-marsh zones of semipermanently flooded wetlands. Species composition of fairy shrimp populations change with increasing salt concentrations of the water column. Amphipods and fairy shrimp are occasionally present in the same wetland. Brine shrimp (Artemia salina) predominate where salt concentrations are >35 mS/cm.

Invertebrates occupying the water column of a prairie wetland complex in the Cottonwood Lake, ND, study area are listed in Table 4. Wetland T8 is seasonally flooded and functions as a ground-water recharge area. Wetland T3 is a seasonally flooded through-flow system. Wetland P1 is a nonintegrated, semipermanent wetland that has no surface outlet and functions as a ground-water discharge area. Wetland P8 is a through-flow, semipermanent wetland that contains a surface outlet. Wetland P11 is a semipermanent wetland that has no surface outlet, functions as a ground-water discharge area, and concentrates salts by loss of water to the atmosphere.

Insects, particularly Coleoptera, Odonata, and Hemiptera, play an important role in the ecology of prairie wetlands by assuming the role of top predators within the water column. Wetland insects differ from the gastropods and crustacea of prairie wetlands in that most are capable of flight and can quickly invade shallow wetlands soon after they receive water. This applies especially to adult Coleoptera; members of this group are found in seasonally flooded wetlands soon after spring snowmelt is complete (Hanson and Swanson 1989).

Descriptions of insects often omit information on habitat. Light traps that attract adults from a relatively large area are routinely used for collecting. This procedure, while efficient for taxonomic studies, cannot be used to associate adults with the types of aquatic habitat that support larvae.

Insects are similar to gastropods and crustacea in that their species structure is influenced by hydroperiod and salinity. A study of the Coleoptera of seasonally and semipermanently flooded wetlands in a Cottonwood Lake wetland complex demonstrated differential use of these wetlands by species (Table 5). Of the 57 species identified, 47 and 38 were collected on seasonally and semipermanently flooded wetlands, respectively (Hanson and Swanson 1987); 18 and 11 species were found only on seasonally and semipermanently flooded wetlands, respectively. Individual species showed preferences for one of the wetland classes even though they occupied both. For example, only one Agabus antennatus was found on seasonally flooded wetlands, compared to 172 specimens collected on semipermanently flooded wetlands. On the other hand, 88 Hydroporous fuscipennis were found on seasonally flooded wetlands, but only 2 on semipermanently flooded wetlands. Of the Coleoptera reported for the State of North Dakota 39% were found

Table 4. Invertebrate taxa, maximum densities, and month(s) of observed maximum density in the water column of seasonal and semipermanent wetlands in the Cottonwood Lake study area, Stutsman County, North Dakota, in 1984 (from LaBaugh and Swanson 1988).

	Seasonal wetlands		Semipermanent wetlands		
	T8	T3	P1	P8	P11
Basin chemical type[a]	$KHCO_3$	$CaSO_4$	$MgSO_4$	$MgHCO_3$	$NaSO_4$
Specific conductivity (mS/cm)	90-144	728-1350	1620-2960	797-1120	3850-7580
Dominant emergents (central zone)	Polygonum coccineum-Carex atherodes	Scolochloa festucacea-Carex atherodes	Typha spp.-Scirpus acutus	Typha spp.-Scirpus acutus	Scirpus maritimus-Scirpus acutus
Copepoda					
Diacyclops bicuspidatus thomasi	330[b] (6)	188 (5)	44 (5)	11 (5)	391 (5)
Diaptomus clavipes			141 (8)	5 (7)	
D. sicilis					359 (9)
Copepod naupli	1287 (6)	703 (6)	343 (6)	115 (6)	191 (5)
Canthocamptus sp.	41 (5)				
Macrocyclops fuscus				3 (9)	
Paracyclops fimbriatus poppei				47 (5)	
Cyclopoid copepodids				29 (5)	65 (10)
Cladocera					
Daphnia pulex	27 (5)	192 (6)	172 (5)	4 (5)	
D. rosea				17 (7)	
D. similis					449 (6)
Immature Daphnia		4 (7)		6 (6)	
Simocephalus vetulus	21 (6)	6 (7)		Tr.[c] (6)	
Ceriodaphnia quadrangula		25 (7)	23 (7)	3 (6)	23 (6)
C. reticulata	666 (6)				
Alona guttata	154 (6)				
Pleuroxus procurvatus				Tr. (6)	
Scapholeberis guritus	19 (7)	37 (6)		3 (7)	
Chydorus sphaericus				5 (6)	
C. sp.		4 (6)	Tr. (6)		1 (7)
Moina macrocalps?					Tr. (5)

(Continued)

Table 4. (Continued).

	Seasonal wetlands		Semipermanent wetlands		
	T8	T3	P1	P8	P11
Basin chemical type[a]	$KHCO_3$	$CaSO_4$	$MgSO_4$	$MgHCO_3$	$NaSO_4$
Specific conductivity (mS/cm)	90-144	728-1350	1620-2960	797-1120	3850-7580
Dominant emergents (central zone)	Polygonum coccineum-Carex atherodes	Scolochloa festucacea-Carex atherodes	Typha spp.-Scirpus acutus	Typha spp.-Scirpus acutus	Scirpus maritimus-Scirpus acutus
Rotifera					
Keratella quadrata			1 (9)	Tr. (9)	155 (8)
K. serrulata	81 (6)	2 (6)			
Polyarthra sp.	111 (6)	1 (6,7)		15 (8)	
Lecane sp.	7 (5)	13 (7)		Tr. (10)	
Euchlanis sp.	12 (5)	5 (6)	Tr. (5)	5 (5)	
Platyias sp.	22 (7)	18 (7)	8 (8)	5 (7)	
Monostyla sp.	10 (7)	8 (7)			
Conochilus sp.	3 (7)	2 (5)			
Accomorpha sp.		8 (5)			
Asplanchna sp.		1 (7)			
Brachionus sp.				Tr. (9)	
Trichocera sp.			1 (5)		
Notholca accuminata				Tr. (7)	
N. sp.					67 (5)
Synchaeta sp.				2056 (5)	10 (8)
Amphipoda					
Hyalella azteca				Tr. (8)	1 (7)
Eubranchiopoda					
Anostraca sp.	3 (5)	1 (5)			
Ostracoda sp.	8 (7)	30 (5)	Tr. (6)	2 (5)	1 (5)
Hydracarina sp.	3 (6)	1 (7)	Tr. (7)	Tr. (7)	
Hemiptera					
Corixidae sp.	4 (6)				
Notonectidae sp.			Tr. (8)	11 (6)	
Coleoptera					
Dytiscidae sp.	4 (6)		Tr. (7,8,9)	Tr. (5)	
Diptera					
Chironomidae sp.	12 (5)	1 (7)	Tr. (5,7,8)	1 (7)	
Chaoborus sp.		1 (7)	Tr. (8,9)	1 (9)	

(Continued)

Table 4. (Concluded).

	Seasonal wetlands		Semipermanent wetlands		
	T8	T3	P1	P8	P11
Basin chemical type[a]	$KHCO_3$	$CaSO_4$	$MgSO_4$	$MgHCO_3$	$NaSO_4$
Specific conductivity (mS/cm)	90-144	728-1350	1620-2960	797-1120	3850-7580
Dominant emergents (central zone)	*Polygonum coccineum*-*Carex atherodes*	*Scolochloa festucacea*-*Carex atherodes*	*Typha* *spp*.-*Scirpus* *acutus*	*Typha* *spp*.-*Scirpus* *acutus*	*Scirpus maritimus*-*Scirpus* *acutus*
Ephemeroptera					
Baetis sp.			Tr. (8)	Tr. (8)	
Odonata					
Zygoptera sp.			Tr. (5)		

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[a] LaBaugh et al. 1987

[b] Densities are expressed as mean organisms/L (n= 3 samples/month) for the month of greatest abundance. Month of greatest abundance is in parentheses; more than one month is shown where monthly abundances were identical. Seasonal wetlands were sampled 3 times per visit each month from May through July; semipermanent wetlands were sampled 3 times per visit each month from May through October.

[c] Tr.= <1 organism/L.

Table 5. Wetland use by aquatic Coleoptera in the Cottonwood Lake study area, Stutsman County, North Dakota, April 1979 - November 1980. Use expressed as a number captured per unit effort (Hanson and Swanson 1989).

	Seasonal wetlands			Semipermanent wetlands		
	T3	T8	Total	P1	P8	Total
Coleoptera	51.5	28.0	40.9	4.7	10.8	7.7
Dytiscidae	35.7	22.5	29.8	3.9	8.8	6.3
Agabus ajax				<0.1	0.2	0.1
Agabus antennatus	<0.1		<0.1	1.1	1.6	1.4
Agabus bifarius	1.8	1.0	1.5	<0.1	<0.1	<0.1
Agabus canadensis	1.1	0.3	0.7			
Agabus falli		0.1	<0.1			
Agabus punctulatus	2.2	2.2	2.2			
Colymbetes sculptilis	2.6	2.6	2.6	0.5	1.3	0.9
Coptotomus longulus	0.1	0.1	0.1		0.2	0.1
Dytiscus alaskanus					<0.1	<0.1
Dytiscus circumcinctus	<0.1		<0.1	<0.1		<0.1
Dytiscus cordieri	0.2		0.1	0.1	<0.1	0.1
Dytiscus hybridus	0.5	0.1	0.3			
Graphoderus occidentalis	1.6		0.9	0.3	0.1	0.2
Graphoderus perplexus				0.1	0.3	0.2
Hydaticus modestus	0.1		0.1	<0.1	0.1	0.1
Hydaticus piceous				<0.1		<0.1
Hydroporous fuscipennis	1.9	2.6	2.2	<0.1		<0.1
Hydroporous notabilis	<0.1		<0.1		<0.1	<0.1
Hydroporous pervicinus	0.3	1.2	0.7			
Hydroporous tenebrosus	0.8	2.3	1.5	<0.1	<0.1	<0.1
Hygrotus acaroides					<0.1	<0.1
Hygrotus canadensis	1.5	0.1	0.8			
Hygrotus compar	0.8	2.3	1.5			
Hygrotus impressopunctatus	2.1	0.2	1.3	0.2	0.1	0.2
Hygrotus patruelis	0.8	2.3	1.5	<0.1	0.3	0.2
Hygrotus picatus				<0.1	<0.1	<0.1
Hygrotus sayi	0.1		0.1	0.1	1.3	0.7
Hygrotus sellatus	0.1	0.1				
Hygrotus turbidus	5.0	0.5	3.0	0.2	0.1	0.2
Ilybius fraterculus				0.1	0.2	0.2
Ilybius biguttulus					0.1	<0.1
Laccophilus biguttatus	1.5		0.8	0.2	1.4	0.8
Laccophilus maculosus	1.0		0.6			
Laccornis conoideus	0.2	0.2	0.2	0.1		<0.1
Liodessus affinis	0.7	0.2	0.5		<0.1	<0.1
Rhantus consimilis		0.4	0.2			
Rhantus frontalis	8.2	4.4	6.5	0.7	0.9	0.8
Rhantus suturellus	0.3		0.2			
Gyrinidae	<0.1		<0.1	0.1	<0.1	0.1
Gyrinus maculiventris	<0.1		<0.1	<0.1		<0.1
Gyrinus minutus				0.1	<0.1	0.1

(Continued)

Table 5. (Concluded).

	Seasonal wetlands			Semipermanent wetlands		
	T3	T8	Total	P1	P8	Total
Haliplidae	1.1	2.6	1.8	0.5	1.8	1.2
Haliplus hoppingi	0.2	2.5	1.3	<0.1		<0.1
Haliplus immaculicollis	0.1		0.1	0.3	1.0	0.6
Haliplus strigatus	0.2	0.1	0.2	0.1	0.7	0.4
Haliplus subguttatus	0.6		0.3	0.1	<0.1	0.1
Peltodytes edentulus					<0.1	<0.1
Peltodytes tortulosus					0.1	<0.1
Hydrophilidae	14.7	2.9	9.4	0.2	0.2	0.2
Berosus fraternus	1.3	1.4	1.4		<0.1	<0.1
Berosus hatchi	8.2	0.3	4.7			
Berosus striatus		0.1	0.1	<0.1		<0.1
Helophorus oblongus		0.3	0.2			
Helophorus linearis		0.1	<0.1			
Helophorus lineatus		0.1	<0.1			
Hydrobius fuscipes		0.3	0.1			
Hydrochara obtusata	0.3	0.2	0.3		<0.1	<0.1
Hydrochus squamifer		0.1	<0.1			
Hydrophilus triangularis	<0.1		<0.1			
Tropisternis lateralis nimbatus	4.7		2.6	0.2	0.1	0.1

on the 97-ha Cottonwood Lake study area (Hanson and Swanson 1989).

Nelson and Butler (1987) examined seasonal abundance of larval chironomids and emergence patterns of adults for two years on two wetland classes on the Cottonwood Lake study area. They found that seasonally flooded wetlands had lower larval densities than semipermanently flooded wetlands, and that densities of emerging adults were lower in the seasonally flooded sites.

Fresh and oligosaline wetlands (Cowardin et al. 1979) in the Prairie Pothole Region support a typical species structure of aquatic invertebrates as described for the United States by Pennak (1978), but as salt concentrations increase, only the most salt-tolerant groups such as the shore flies (Ephydridae) persist.

3.4 FISH

The subject of fish use of prairie wetlands has recently been reviewed by Peterka (1989). He states that fathead minnows (*Pimephales promelas*) and brook sticklebacks (*Culaea inconstans*) are the only two native fishes that can tolerate shallow water depths (<5m), low dissolved-oxygen concentrations, and occasional high concentrations of sulfates and bicarbonates found in these wetlands. Low dissolved oxygen concentrations cause both winterkill and summerkill. He also noted that most wetlands in the region lie in closed drainage basins, thereby limiting fish dispersal. Fish are limited to an even greater extent in the wetlands dealt with in this report, as only palustrine systems and lacustrine littoral systems, which extend to a depth of 2 m below low water, are included.

Fish cannot survive year round in temporary or seasonal wetland basins in the Prairie Pothole Region, because these wetlands dry out or freeze completely or nearly to the bottom each winter. Interpolated data of Schoenecker (1970) and Barica (1979) for Nebraska and Manitoba, respectively, indicate that wetlands in the Dakotas remain frozen for about 4-5 months each year with maximum ice depths of about 0.7-0.8 m. It is likely that a few temporary and seasonal basins with riparian connections to more permanent wetlands receive an influx of fish in the spring during years of high water levels, but unless water levels are maintained, these fish will soon perish. It is also possible that some temporary or seasonal wetlands are temporarily stocked with fish, fry, or eggs by waterbirds, but this method of dispersal is undocumented (Peterka 1989).

Only in the few semipermanent wetland basins with reliable connections to deepwater habitat or other refugia can one expect to find fish, unless they have been introduced. Lawler et al. (1974) found fathead minnows and brook sticklebacks in 10%-20% of the wetlands in the prairie region of Manitoba, but if the wetlands that contained water >2 m deep had been eliminated from this sample, the percentages would undoubtedly have been much lower.

Wetlands where fish survive in high-water years can lose all fish when low water levels prevail. In some of these wetlands, refugia from winterkill can be provided by ground-water seepage areas where some oxygen is present (Peterka 1989).

Fish survival in a few semipermanent wetlands can be limited by excess dissolved solids, as well as shallowness and low supplies of dissolved oxygen at various times of the year. Total dissolved solids concentrations of 17,000-18,000 mg/l seem to be the approximate upper limit for survival of native fish in magnesium sulfate and sodium chloride type waters in the prairie region (Rawson and Moore 1944; Burnham and Peterka 1975). For sodium sulfate and sodium bicarbonate type waters, 12,000 mg/l and 2,000 mg/l seems to be the upper limits (Held and Peterka 1974; McCarraher 1971).

3.5 AMPHIBIANS AND REPTILES

According to Wheeler and Wheeler (1966), the herpetofauna of South Dakota includes 40 species (12 amphibians and 28 reptiles), and of North Dakota, only 25 species (11 amphibians and 14 reptiles). Of these, only the tiger salamander (*Ambystoma tigrinum*), American toad (*Bufo americanus*), Great Plains toad (*B. cognatus*), Dakota toad (*B. hemiophrys*), Rocky Mountain toad (*B. woodhousei*), chorus frog (*Pseudacris nigrita*), leopard frog (*Rana pipiens*), wood frog (*R. sylvatica*), painted turtle (*Chrysemys picta*), plains garter snake (*Thamnophis radix*), and red-sided garter snake (*T. sirtalis*) use prairie basin wetlands. The only species intimately associated with these wetlands are the tiger salamander, leopard frog, and chorus frog.

Tiger salamanders are biologically well adapted to the dynamic physical and chemical characteristics of prairie wetlands, while major aquatic predators and competitors such as fish are poorly adapted to their harsh chemical environment and recurring drought (Peterka 1989). Larval tiger salamanders have been collected in West Stump Lake, ND, in water with specific conductivities of 12.5 mS/cm (Deutschman and Peterka 1988). Larval densities in North Dakota wetlands can exceed 5,000/ha and maximum annual production of 565 kg/ha has been recorded (Deutschman and Peterka 1988). Salamander larvae at high densities are an important component in the energy flow of the wetlands they inhabit.

Amphipods (*Gammarus lacustris*) accounted for 78% of the volume of food items in stomach contents of salamanders in North Dakota (Myers 1973). *Gammarus* spp. tend to occupy wetlands that function as through-flow systems; these wetlands are relatively stable and low in salts. Large salamander larvae (neotenics) occasionally overwinter in wetlands and at this time can impact the invertebrate community.

Aquatic birds that normally feed on fish also feed on larval salamanders. Wiedenheft (1983) reported finding wounds on the dorsal surface of the tails of 10% of a salamander population. Potential predators include the grebes, herring gulls (*Larus argentatus*), American white pelicans (*Pelecanus erythrorhynchos*), double-crested cormorants (*Phalacrocor axauritus*), and black-crowned night-herons (*Nycticorax nycticorax*).

Leopard frogs have an immense range in North America. On the Dakota prairies, these frogs seem to prefer temporary and seasonal wetlands for courtship activities, but lay most of their eggs in semipermanent wetlands where the tadpoles require about 3 months to metamorphose into adults.

The diminutive chorus frog is found over most of North America. The frogs congregate to breed in the early spring in seasonal and semipermanent wetlands. After breeding, they wander away from water bodies, but still require damp places to avoid desiccation.

3.6 BIRDS

Waterfowl

The North American Prairie Pothole Region produces the bulk of North America's duck population. Smith et al. (1964) estimated that the region, comprising only 10% of the waterfowl breeding area of the continent, produces 50% of the ducks in an average year, and more than that when good water conditions prevail. About 23% of the Prairie Pothole Region lies in the Dakotas. Many wetlands in the region are also important fall staging and migration areas (Kantrud 1986b). The open, shallow wetlands found in cultivated fields are also heavily used by spring migrant waterfowl. For example, arctic-nesting geese stop in the Prairie Pothole Region to fatten while enroute to their breeding grounds (Alisauskus 1988). Availability of shallow wetlands in open, agricultural landscapes also allows the birds to disperse widely, thereby reducing or eliminating potential hazards from disease, particularly avian cholera (G. Krapu, pers. comm.).

Faanes and Stewart (1982) list 23 species of Anatidae that have nested at least once in North Dakota. The trumpeter swan (*Cygnus buccinator*), white-winged scoter (*Melanitta fusca*), and common merganser (*Mergus merganser*) have been extirpated as breeding species in the state. The snow goose (*Chen caerulescens*) is listed as an occasional breeder, but has nested only once in the state, and that under unusual circumstances. Rare breeders include the American black duck (*Anas rubripes*), cinnamon teal (*Anas cyanoptera*), common goldeneye (*Bucephala clangula*), and bufflehead (*B. albeola*).

The remaining 15 species are well-established breeders in the Prairie Pothole Region of North Dakota. These include the Canada goose (*Branta canadensis*), wood duck (*Aix sponsa*), green-winged teal (*Anas crecca*), mallard (*A. platyrhynchos*), northern pintail (*A. acuta*), blue-winged teal (*A. discors*), northern shoveler (*A. clypeata*), gadwall (*A. strepera*), American wigeon (*A. americana*), canvasback (*Aythya valisineria*), redhead (*A. americana*), ring-necked duck (*A. collaris*), lesser scaup (*A. affinis*), hooded merganser (*Lopodytes cucullatus*), and ruddy duck (*Oxyura jamaicensis*).

Bufflehead and common goldeneye do not breed in South Dakota (Whitney et al. 1978). The trumpeter swan has been restored as a breeding species in the state, but not in the Prairie Pothole Region. The American black duck, hooded merganser, and common merganser are rare, but probably breed in the state. Cinnamon teal breed regularly west of the Missouri River in South Dakota, but are rare in the Prairie Pothole Region, leaving 14 species of waterfowl as well-established breeders in the Prairie Pothole Region of South Dakota.

In 1973-74, about 69%-79% of an estimated 439,600 to 1,067,500 pairs of breeding waterfowl in South Dakota were located in the pothole region (Brewster et al. 1976). The proportion of birds in the region was undoubtedly much higher before the construction of thousands of dams and dugouts for livestock watering facilities in the western part of the state.

Stewart and Kantrud (1973) estimated that about 84% of 2,281,000 pairs of breeding waterfowl were located in the pothole region of North Dakota in 1967. This region comprises 51.5% of the state area. They estimated that the breeding waterfowl population in the pothole region of the state averaged about 1,600,000 pairs (995,000-1,955,000 pairs) during 1967-69.

Because prairie wetlands are of extreme importance to an international resource, the numbers of breeding, molting, staging, and migrating waterfowl observed in these basins, and the foods consumed by these birds in various stages of their life cycle, have received considerable attention by wildlife biologists. A current review of these topics is available (Swanson and Duebbert 1989). The temporary, seasonal, and semipermanent wetlands dealt with in this report are by far the most important types of wetlands for most species of waterfowl that breed in the Dakotas and throughout the Prairie Pothole Region.

Wetland use by waterfowl can be expressed in various ways. Use expressed on an area basis results in high relative values for small basins, whereas use expressed on a wetland unit basis results in relatively high values for large basins, even though many large basins have large central areas of open water that may receive little use. Use of basins by breeding waterfowl has also been expressed in pairs per unit length of shoreline. This also tends to result in high values for small basins. Waterfowl use of basins has also sometimes been expressed in terms of basin area without regard to the presence or absence of surface water (Kantrud and Stewart 1977). This is done in attempts to evaluate an entire wetland class, not only those basins within a class that happen to contain ponded water at any particular time.

<ins>Temporary wetland basins</ins>. The primary function of these wetlands is to provide isolation for breeding pairs and supply invertebrate foods for waterfowl early in the nesting period. The rapid warming of these shallow wetlands in the spring results in early development of invertebrate populations (Swanson et al. 1974). Temporary basins, especially those containing flooded crop residues, receive considerable use by spring migrant waterfowl, but are usually dry during the fall migration period. Nevertheless, these basins are occasionally filled by fall rains, in which case they may be used to a considerable extent by fall migrant dabbling ducks.

Up to 6.8% of the South Dakota breeding population can be found on these basins when water conditions are relatively good, and the water ponded there makes up about 4% of the surface water available in all wetlands (Ruwaldt et al. 1979). About 2%-4% of the breeding waterfowl population was observed on temporary wetlands in North Dakota during the 1967-69 seasons (Stewart and Kantrud 1973). For both of these studies, the proportional use of the basins was underestimated because many intensively tilled wetlands, many undoubtedly of the temporarily flooded water regime, could not be classified as to water regime.

Cowardin et al. (1988 and unpubl. data) used wetland data from the late 1970's to early 1980's and waterfowl pair counts from the mid-1980's to estimate the density of five common species of breeding dabbling ducks in various classes of wetland basins during a wet year in the Dakotas. This analysis showed that 9.9%-13.4% of the mallards, 6.7%-10.6% of the gadwall, 4.3%-6.3% of the bluewinged teal, 7.7%-11.2% of the northern shoveler, and 13.3%-17.1% of the northern pintail populations could be expected to be found on temporary wetlands. The relatively greater use of temporary wetlands by early-nesting species, mallard and northern pintail, is in agreement with the food-habit studies of Swanson et al. (1985) for the mallard and Krapu (1974a, b) for the northern pintail. These studies showed that temporary wetlands are a major source of the animal protein needed by nesting hens to produce clutches of viable eggs. Poor-quality diets lead to reduced clutch and egg size, laying rate, and number of nesting attempts (Eldridge and Krapu 1988). That mallard breeding populations correlate better with acreages of water 15 cm or more deep than with acreages of water 30 or 46 cm or more deep provides further evidence of the importance of shallow water to early-nesting species (Stewart and Kantrud unpubl.).

Temporary basins are used only by breeding dabbling ducks (Anatini) in the Dakotas. Use of these basins decreases greatly during relatively dry springs, as ponded water can be absent or maintained for only a few weeks. In South Dakota, the greatest pair densities on these wetlands, on the basis of both basin area and basin unit, were, in decreasing order of magnitude, found for blue-winged teal (*Anas discors*), northern pintail (*A. acuta*), mallard (*A. platyrhynchos*), northern shoveler (*A. clypeata*), green-winged teal (*A. crecca*), and gadwall (*A. strepera*) (Ruwaldt et al. 1979).

Very similar results were reported by Kantrud and Stewart (1977) for temporary basins in North Dakota. They also observed use of these basins by small numbers of American wigeon (*A. americana*). They found that, on the basis of area of basins with surface water, temporary wetlands showed greater use by dabbling ducks (364.2 pairs/km^2) than any other wetland class. But when all basins were considered without regard to the presence or absence of surface water, temporary basins supported 126.6 pairs/km^2. This was only about 47% and 79% of the dabbling duck density found on seasonal and semipermanent wetlands, respectively.

Seasonal wetland basins. These basins are a major source of invertebrate protein for laying female ducks early in the breeding season, and also provide isolation for pairs and sites for overwater nests. During wet years, these basins are also highly attractive as brood habitat (Talent et al. 1982) and molting areas. Seasonal wetlands usually receive considerable use by spring migrant waterfowl, but normally are dry by fall and little used by fall migrants unless unusually wet conditions prevail. Under these circumstances, seasonal wetlands can be heavily used by dabbling ducks, especially those species that regularly feed in upland grainfields.

During May and June of relatively wet years, 14.5%-16.2% of the breeding population can be found on seasonal basins in South Dakota. These basins contain 9.8%-11.0% of the surface water available in all wetlands under these conditions (Ruwaldt et al. 1979). In North Dakota, over 47% of the breeding duck population was observed on these basins over a three-year period (Stewart and Kantrud 1973). Again, the proportion of the waterfowl population that was observed on these basins is underestimated in both these studies, because of the difficulty of classifying intensively tilled wetlands early in the growing season.

Because of their greater average depth and water-holding ability, seasonal basins are used by breeding diving ducks (Aythyini) and stiff-tailed ducks (Oxyurini), as well as dabbling ducks. In recent years, use of seasonal wetland basins near wooded areas by wood ducks (Aix sponsa, tribe Cairinini) has also increased in the Dakotas.

On the basis of both basin area and basin unit, seasonal wetlands in South Dakota received the greatest use by blue-winged teal, followed in decreasing order by mallard, northern pintail, gadwall, northern shoveler, redhead (Aythya americana), green-winged teal, ruddy duck (Oxyura jamaicensis), and American wigeon (Ruwaldt et al. 1979).

Seasonal basins are used even more heavily in North Dakota, where diving ducks are more abundant and widespread than in South Dakota. In addition to the species recorded in seasonal basins in South Dakota by Ruwaldt et al. (1979), similar basins in North Dakota also supported lesser scaup (Aythya affinis), canvasback (A. valisineria), and ring-necked duck (A. collaris) (Kantrud and Stewart 1977). As in South Dakota, the main users of seasonal wetlands were blue-winged teal, northern pintail, mallard, gadwall, and northern shoveler. Kantrud and Stewart (1977) also found that, on the basis of basins with ponded water, classifiable seasonal wetlands in North Dakota supported 317.2 pairs of dabbling ducks per square kilometer and 16.6 pairs/km^2 of combined diving and stiff-tailed ducks. Unclassifiable, intensively tilled wetland basins, many of which are also likely of the seasonal water regime, supported 193.2 pairs/km^2 dabbling ducks and 6.8 pairs/km^2 of combined diving and stiff-tailed ducks. They also observed that, when the presence or absence of surface water was not considered, seasonal wetland basins supported a greater density (287.2 pairs/km^2) of breeding waterfowl than any other class of natural basin wetland.

Semipermanent wetland basins. These basins supply most of the needs of all common prairie-nesting waterfowl and their broods. Use of semipermanent wetlands by breeding waterfowl seems to be greatest when amounts of emergent cover and open water are approximately equal (Weller and Spatcher 1965). Schultz (1987) showed that livestock grazing of Typha stands in semipermanent wetlands could result in a tenfold increase in pairs of breeding ducks. Use by broods can increase greatly during years when seasonal wetlands are dry (Talent et al. 1982). A notable exception to the relatively high use of these wetlands occurs in early spring. Semipermanent wetlands are among the last to become ice-free in the spring, and thus they do not provide an early source of invertebrate foods for nesting dabbling duck hens, particularly those that can begin nesting in late March or April.

Semipermanent wetlands are also the main general habitat for staging and fall migrant waterfowl in the Dakotas and the rest of the Prairie Pothole Region, although intermittently exposed and permanently flooded lacustrine wetlands are most heavily used by certain species.

Use of semipermanent wetland basins by dabbling ducks increases during the breeding season. In South Dakota during 1973-74, Ruwaldt et al. (1979) found 24.8%- 26.6% and

41.7%-47.2%, respectively, of the May and June breeding duck population on these basins. During these months semipermanent basins accounted for 35%-42% of the surface-water area in the state. Semipermanent wetlands composed 18% of the area and 3% of the number of all wetlands, and 16% of the breeding duck population was found on these basins in the Prairie Pothole Region of North Dakota in 1967 (Stewart and Kantrud 1973). The following year was relatively dry, and 41% of the breeding duck population was observed on semipermanent wetlands.

Although the proportion of the breeding duck population found on semipermanent basins can increase greatly during relatively dry years, duck densities on these basins can decrease. Ruwaldt et al. (1979) observed 6.73 duck pairs per wet basin (2.57 pairs/ha) when water conditions were good and the water in the basins made up 42.3%- 44.6% of the surface water area. At this time, 24.8%-41.7% of the total duck population was observed on these basins. During the following relatively dry year these basins still held 35.6% of the available surface water, but duck densities in them fell to 3.6 pairs per wet basin (2.07 pairs/ha). At this time, 26.6%-47.2% of the duck population was found on these basins. This phenomenon is presumably caused by the lack of enough water to produce foods in nearby temporary and seasonal basins (Krapu 1974a, Swanson et al. 1974) and the loss of surface water in the shallow wet-meadow and shallow-marsh zones of the semipermanent wetlands themselves. Northern pintail, blue-winged teal, and northern shoveler seem particularly subject to such annual declines in density in semipermanent basins (Ruwaldt et al 1979). Annual population densities of these species have been shown to be highly correlated with the frequency and area of wetlands containing surface water in North Dakota (Stewart and Kantrud 1974).

When water conditions are good in South Dakota, semipermanent wetland basins support the highest densities of blue-winged teal, followed in decreasing order by the mallard, northern pintail, gadwall, redhead, northern shoveler, ruddy duck, green-winged teal, and American wigeon (Ruwaldt et al. 1979). In North Dakota, highest pair densities on ponded semipermanent basins on the basis of area were also recorded for blue-winged teal, followed in decreasing order by redhead, gadwall, mallard, ruddy duck, northern pintail, northern shoveler, canvasback, green-winged teal, lesser scaup, ring-necked duck, and American wigeon (Kantrud and Stewart 1977). Use by all dabbling ducks and combined diving and stiff-tailed ducks was 189.1 pairs/km^2 and 73.2 pairs/km^2, respectively.

Semipermanent wetland basins are the principal breeding habitat for diving and stiff-tailed ducks in the Dakotas. During 1973-74, these basins supported 72.2%-100% of the populations of these birds in South Dakota (Ruwaldt et al. 1979). In North Dakota, 74.9% of these birds were found on semipermanent basins during 1967-69 (Kantrud and Stewart 1977). The redhead, canvasback, and ruddy duck nearly always nest over water in emergent vegetation in these wetlands, whereas nests of the lesser scaup and ring-necked duck are usually found in adjacent wet meadows. Redheads often lay their eggs in the nests of other overwater-nesting ducks.

Breeding waterfowl obtain most of their foods from wetlands, although field feeding in upland habitats is common during both spring and fall migration. Food consumption by adult and juvenile Anatini (dabbling ducks), Aythyinae (diving ducks), and Oxyurini (ruddy duck) during the breeding season in the Prairie Pothole Region was recently reviewed by Swanson and Duebbert (1989).

Food consumption varies greatly among species and between sexes of adults of a species; it also depends largely on relative availability of the food items as well as the wetland type, salinity, and vegetative zone of the wetlands where the birds were collected. For these reasons, only a superficial account of this complex subject can be presented here.

Consumption of invertebrates by the most common species of laying female Anatini is very high, varying from 72% by volume for the gadwall and mallard to 99% by volume for the northern shoveler and blue-winged teal. Foods of male Anatini during the breeding season vary from 70% seeds by volume for northern pintail to 97% invertebrates by volume for northern shoveler.

Juvenile Anatini of all species, especially during the first few weeks of growth, rely heavily on animal foods. All species investigated to date consume large amounts of either Insecta, Crustacea or Mollusca. Exceptions are older juvenile gadwall and American wigeon, which consume mostly vegetable material.

Adult female Aythyini and Oxyurini also rely heavily on invertebrate foods during the laying period. Consumption varies from a low of 70% by volume for the redhead to a high of 99% by volume for the ruddy duck (Woodin and Swanson 1989). Chironomidae (Diptera) are important for several species. Invertebrate use by most breeding male Anatini is similar to the females. An exception is the canvasback, which consumes about 98% vegetable foods by volume during the breeding period.

Nearly all juvenile Aythyini and Oxyurini studied to date consume 80% or more invertebrates, by either weight or volume, mostly Amphipoda, Trichoptera, and Diptera. The only exception is the redhead, which Bartonek and Hickey (1969) showed to consume 43% invertebrates by volume.

Other Marsh and Aquatic Birds

Approximately 39% of the 353 valid species on the North Dakota bird list (Faanes and Stewart 1982) use wetlands. Of the 223 species with known or inferred breeding status in North Dakota, 57 (26%) are marsh or aquatic birds other than waterfowl.

Of these 57 species, the spectacular whooping crane (Grus americana) has been extirpated as a breeding bird in the state. Distribution of nests and records of adults during the breeding season indicate this species once nested throughout the Prairie Pothole Region of North Dakota (Stewart 1975).

Of the 56 remaining species, 15 are generally not associated with the shallow-basin wetlands dealt with in this report, although many of them can be seen resting or feeding in or around these wetlands, both during the breeding season and in migration. This group is composed of the common loon (Gavia immer), red-necked grebe (Podiceps grisegena), osprey (Pandion heliaetus), bald eagle (Haliaeetus leucocephalus), yellow rail (Coturnicops noveboracensis), common snipe (Gallinago gallinago), American woodcock (Scolopax minor), ring-billed gull (Larus delawarensis), California gull (Larus californicus), Caspian tern (Sterna caspia), common tern (S. hirundo), least tern (S. antillarum), belted kingfisher (Ceryle alcyon), willow flycatcher (Empidonax traillii), and swamp sparrow (Melospiza georgiana).

There are eight rare to uncommon species that likely nest, have nested, or are inferred to nest in vegetative zones found in wetlands dealt with in this report, but little is known of their habitat use. This group of birds includes the least bittern (Ixobrychus exilis), little blue heron (Egretta caerulea), tricolored heron (Egretta tricolor), cattle egret (Bubulcus ibis), green-backed heron (Butorides striatus) king rail (Rallus elegans), sandhill crane (Grus canadensis) and white-faced ibis (Plegadis chihi). The sandhill crane likely was a fairly common breeding species in North Dakota before the turn of the century (Stewart 1975).

An additional 11 fairly common to abundant species regularly breed or nest in various vegetative zones found in wetlands dealt with in this report, but little quantitative habitat use information is available for these birds. These species include the American white pelican (Pelecanus erythrorhynchos), double-crested cormorant (Phalacrocorax auritus), great blue heron (Ardea herodias), Franklin's gull (Larus pipixican), spotted sandpiper (Actitis macularia), Forster's tern (Sterna forsteri), sedge wren (Cistothorus platensis), Le Conte's sparrow (Ammodramus leconteii), sharp-tailed sparrow (Ammodramus caudacutus), song sparrow (Melospiza melodia), and common grackle (Quiscalus quiscula).

For the remaining 22 species, a fair amount of information is available on use of wetland habitat in North Dakota. These 22 species are most characteristic of the wetlands dealt with in this report; the distribution of 21 of them among the subject wetlands is shown in Table 6. Nearly two-thirds of the total population were found on semipermanent wetlands, and all species used this wetland class. For 11 species, over half the population was found on semipermanent wetlands. Seasonal wetlands were used by 20 species and supported about one-third of the total population. From 53% to 64% of the population of seven of the species occupied seasonal wetlands. Temporary and undifferentiated-tillage wetlands were of little importance to the birds listed.

Densities are expressed in pairs per square kilometer in Table 7. These are crude measurements of density because they are based on the entire wetland, rather than on specific zones or plant communities used by the birds. On this basis, the highest densities of birds occurred on semipermanent wetlands. These wetlands are especially attractive to American coot and black tern. Temporary wetlands supported high densities of red-winged blackbirds and savannah sparrows. Killdeer and marbled godwit were also found in greatest densities on these wetlands, although most of the use was of shoreline areas. Horned grebe, eared grebe, and willet were especially dense on seasonal wetlands. Agricultural use of wetlands obviously decreased their value to most species except for the American avocet and Wilson's phalarope, both of which reached highest densities on wetlands with frequently tilled soils.

Faanes (1982) censused breeding birds of all species in seasonal and semipermanent basin wetlands and other habitat types in a study area in central North Dakota during April-June 1980. He recorded 1357.8 pr/km^2 in semipermanent wetlands. This density was exceeded only in shelterbelts (2658.7 pr/km^2). Seasonal wetlands supported 574 pr/km^2. This density was exceeded only by shelterbelts, semipermanent wetlands, and prairie thickets (878.5 pr/km^2).

Faanes (1982) also found the highest nesting or breeding densities of Forster's tern, red-winged blackbird, and brown-headed cowbird (Molothrus ater) in semipermanent wetlands, and noted that breeding song sparrows also used the periphery of this wetland class. He also observed breeding pairs of bobolink (Dolichonyx orzivorous), savannah sparrow, and sharp-tailed sparrow in seasonal wetlands.

Information on frequency of use of temporary, seasonal, and semipermanent wetlands was gathered for 13 selected nonwaterfowl species in

Table 6. Percentage distribution of breeding marsh and aquatic birds in North Dakota wetlands in 1968-69 (from Kantrud and Stewart 1984).[a]

Species	Wetland class[b]			
	2	3	4	T
Horned grebe (*Podiceps auritus*)		64	36	
Eared grebe (*Podiceps nigricollis*)		54	34	
Western grebe (*Aechmophorus occidentalis*)			5	
Pied-billed grebe (*Podilymbus podiceps*)		23	68	
Black-crowned night heron (*Nycticorax nycticorax*)		6	75	
American bittern (*Botaurus lentiginosus*)	2	30	69	
Northern harrier (*Circus cyaneus*)		23	77	
Virginia rail (*Rallus limicola*)		14	86	
Sora (*Porzana carolina*)	1	45	54	
American coot (*Fulica americana*)	tr[c]	24	72	
Killdeer (*Charadrius vociferus*)	4	53	39	
Willet (*Catoptrophorus semipalmatus*)	2	56	39	
Marbled godwit (*Limosa fedoa*)	3	57	37	
American avocet (*Recurvirostra americana*)		38	47	7
Wilson's phalarope (*Phalaropus tricolor*)	4	60	30	3
Black tern (*Chlidonias niger*)	tr	25	72	
Marsh wren (*Cistothorus palustris*)		9	91	
Common yellowthroat (*Geothlypis trichas*)		48	52	
Yellow-headed blackbird (*Xanthocephalus xanthocephalus*)	tr	6	94	
Red-winged blackbird (*Agelaius phoeniceus*)	2	61	35	
Savannah sparrow (*Passerculus sandwichensis*)	10	49	38	
Total birds	1	33	63	tr

[a] Total percentages across rows subtracted from 100 = the proportion of populations of these species that used wetland classes not covered in this report.

[b] Temporary (Class 2), seasonal (Class 3), semipermanent (Class 4), and undifferentiated tillage (Class T) wetlands.

[c] tr = <0.5%.

Table 7. Density (pairs/km^2) of breeding marsh and aquatic birds in North Dakota wetlands in 1965 and 1968-69 (from Kantrud and Stewart 1984).

	Wetland class[a]			
Species	2	3	4	T
Horned grebe		1.4	0.6	
Eared grebe		3.9	1.9	
Western grebe			0.2	
Pied-billed grebe		5.4	11.9	
Black-crowned night heron		0.4	4.2	
American bittern	5.8	3.3	5.8	
Northern harrier		0.6	1.5	
Virginia rail		0.4	1.8	
Sora	10.1	12.9	12.6	
American coot	25.2	73.8	180.5	
Piping plover (Charadrius melodus)			0.2	
Killdeer	20.6	7.2	5.3	
Willet	10.1	12.3	7.0	
Marbled godwit	10.1	6.9	3.6	
American avocet		3.2	3.2	26.8
Wilson's phalarope	45.4	28.9	11.5	62.5
Black tern	5.8	19.0	44.9	
Marsh wren		4.9	43.8	
Common yellowthroat		7.9	7.8	
Yellow-headed blackbird	11.1	18.1	253.3	
Red-winged blackbird	300.0	99.8	106.8	
Savannah sparrow	188.9	21.5	15.4	
Total	633.1	431.8	723.8	89.3

[a] Temporary (Class 2), seasonal (Class 3), semipermanent (Class 4) and undifferentiated tillage (Class T) wetlands.

South Dakota in 1975 and 1976 (Weber et al. 1982). Among the wetland classes listed (Table 8), the highest frequencies for eight species occurred in semipermanent wetlands that were used by 92% of the species. Seasonal wetlands were used by 85% of the species, and most frequently by the black-crowned night heron and Wilson's phalarope. Temporary wetlands were used by 54% of the species and most frequently by the American avocet, lesser yellowlegs and marbled godwit.

Very little information is available on use of prairie wetlands by migrants and summer visitors. Cultivated and non-cultivated seasonal and temporary wetlands provide habitat for millions of arctic- and subarctic-nesting shorebirds that pass through the Prairie Pothole Region each spring. Ten species of shorebirds studied in North Dakota foraged primarily on crustaceans and insects in these shallow basins during spring migration (Eldridge and Krapu in prep.). In one study area in central North Dakota, Faanes (1982) found use of semipermanent wetlands by white pelican, great blue heron, tundra swan (Olor columbianus), bufflehead, California

Table 8. Frequency of occurrence of 13 selected species of marsh and aquatic birds in South Dakota wetlands during May and June surveys in 1975-76 (from Weber et al. 1982).

Species	Wetland class[a]		
	2	3	4
American bittern		0.8	6.3
Great blue heron			1.2
Green-backed heron			0.4
Black-crowned night heron		3.3	1.2
Sora		3.4	5.5
American avocet	1.4	0.4	
Lesser yellowlegs	2.7	1.9	1.6
Willet	4.1	3.4	4.7
Marbled godwit	4.1	1.5	2.3
Wilson's phalarope	8.2	9.8	7.4
Black tern		1.1	6.3
Yellow-headed blackbird	2.7	6.8	37.5
Red-winged blackbird	37.0	51.9	74.2

[a] Temporary (Class 2), seasonal (Class 3) and semipermanent (Class 4) wetlands.

gull, ring-billed gull, and rusty blackbird (Euphagus carolinus) to be equal to or greater than other wetland types. Similar data for seasonal wetlands indicated high use of these basins by greater yellowlegs (Tringa melanoleucus), solitary sandpiper (T. solitaria), short-billed dowitcher (Limnodromus griseus), Baird's sandpiper (Calidris bairdii), pectoral sandpiper (C. melanotos), stilt sandpiper (Micropalma himantopus), and water pipit (Anthus spinoletta). The highly variable water conditions that prevail across the region emphasize the need to maintain a widely dispersed and intact base of shallow basins to serve the function of spring migration habitat, as deep water does not provide an available invertebrate food source for birds that are morphologically adapted to feeding in shallow water.

A discussion of the use of prairie wetlands by birds would not be complete without mention of the importance of these basins to wintering populations of ring-necked pheasant (Phasianus colchicus). There are no quantitative data on this subject for the Dakotas, but it is obvious to anyone familiar with the habits of this species that it readily seeks the thermal cover and protection from predators and hunters afforded by the dense stands of emergent hydrophytes. There are large areas in both states where wetlands provide pheasants nearly the only protection available from the harsh winter winds common to the northern prairies. This species is an important game bird in both Dakotas. In 1986, 42,000 hunters harvested an estimated 122,000 birds in North Dakota (Grondahl 1987). An estimated 800,000 birds were harvested in South Dakota in 1985 (Ron Fowler, South Dakota Game, Fish and Parks Dept., pers. comm.).

3.7 MAMMALS

Historic Use of Prairie Wetlands

There can be little doubt that the activities of the wild bison (Bison bison), which was extirpated from the Prairie Pothole Region of the Dakotas in the 19th century, had a major biotic influence on prairie wetlands in pristine times. Unfortunately, there is no documentation of how wetlands were impacted by the feeding, drinking, dusting, or other activities of millions of these huge, shaggy beasts as they roamed the prairies. Other grassland mammals extirpated from the region are the grizzly bear (Ursus arctos), kit fox (Vulpes velox) and plains wolf (Canis lupus). These carnivores probably made only minor use of prairie wetlands.

Uncounted numbers of wapiti (Cervus elephus) and pronghorn (Antilocapra americana) and smaller numbers of mule deer (Odocoileus hemionus), the only other large herbivores of open grasslands, once inhabited the region and undoubtedly used the wetlands, at least for drinking. These three species are still found in small numbers in the region. Also nearly extirpated from the prairie region are the river otter (Lutra canadensis), mountain lion (Felis concolor), lynx (F. lynx), and bobcat (F. rufus). Although once distributed throughout the region, it is unlikely that any of these species were strongly associated with the wetlands dealt with in this report.

Modern Use of Prairie Wetlands

A review of modern use of prairie wetlands by mammals has recently been completed by Fritzell (1989). He states that no mammals other than muskrats (Ondatra zibethicus) are typically considered major elements of prairie wetland ecosystems, but cites strong evidence to show that wetlands are vital to many prairie mammals. He lists 17 species of terrestrial or semiaquatic mammals whose geographic range encompasses most of the Prairie Pothole Region and which commonly use wetlands for cover or obtain a substantial portion of their food from wetland-dependent organisms. He also mentions several other species that have been trapped in small numbers in prairie wetlands. We have added species to his list and added information on range and habitat use. The latter was presented in Jones et al. (1983) in an attempt to categorize mammals into groups, often arbitrary, that would indicate the degree of dependence of current wild mammals upon basin wetlands in the region (Table 9). Only wild mammals in Groups 1 and 2 will be discussed in this report.

In the following discussions note that all data on the sale of North and South Dakota pelts by hunters and trappers are for in-state sales only, resulting in a probable understatement of their total worth.

Pelts of the beaver have been sought after since the opening of the region to the fur trade in the 18th century. Beaver occasionally occupy semipermanent wetlands in the Prairie Pothole Region of the Dakotas, especially basins in the northwestern portion of the region where aspen (Populus tremuloides) is sometimes common in the wet-meadow zone and adjacent uplands (A.B. Sargeant, Northern Prairie Wildlife Research Center, pers. comm.), but even there drought can cause mass emigration or decimate populations. Fritzell states that beaver are occasionally reported, but do not establish permanent breeding populations in semipermanent wetlands in the southern portion of the region.

This species occupies primarily riverine wetlands in the region. Populations have increased in recent years, but, compared to its former abundance, beaver numbers are still relatively low. Beaver often cause extensive damage to shade and ornamental trees where rivers flow through residential areas; their dam-building activities can also cause nuisances along watercourses, and offending animals usually are quickly destroyed.

The beaver is a moderately important furbearer in the Dakotas. Dealer surveys indicate an average of 9,025 animals were sold annually

Table 9. General current use of basin wetlands in the Prairie Pothole Region of the Dakotas by wild mammals.

Group and Definition	Common name	Scientific name
1. Depends on wetlands with surface water to complete life cycle	Beaver	*Castor canadensis*
	Muskrat	*Ondatra zibethicus*
	Mink	*Mustela vison*
2. Range encompasses >10% of the region; makes extensive seasonal use of wetlands or likely can complete life-cycle in wet-meadow zones	Arctic shrew	*Sorex arcticus*
	Masked shrew	*Sorex cinereus*
	Pygmy shrew	*Microsorex hoyi*
	Eastern cottontail	*Sylvilagus floridanus*
	Snowshoe hare	*Lepus americanus*
	Western harvest mouse	*Reithrodontomys megalotis*
	Meadow vole	*Microtus pennsylvanicus*
	Meadow jumping mouse	*Zapus hudsonius*
	Western jumping mouse	*Zapus princeps*
	Coyote	*Canis latrans*
	Red fox	*Vulpes vulpes*
	Raccoon	*Procyon lotor*
	Long-tailed weasel	*Mustela frenata*
	Least weasel	*Mustela nivalis*
	Striped skunk	*Mephitis mephitis*
	White-tailed deer	*Odocoileus virginianus*
3. Upland species whose range encompasses >10% of region; likely cannot complete life-cycle in wetlands, but occasionally seen in or over them	Virginia opossum	*Didelphis virginiana*
	Northern short-tailed shrew	*Blarina brevicauda*
	Vespertilionid bats	(Chiroptera: *Vespertilionidae*)
	White-tailed jackrabbit	*Lepus townsendii*
	Franklin's ground squirrel	*Spermophilus franklinii*
	Thirteen-lined ground squirrel	*Spermophilus tridecemlineatus*
	Plains pocket gopher	*Geomys bursarius*
	Deer mouse	*Peromyscus maniculatus*
	Northern grasshopper mouse	*Onocomys leucogaster*

(Continued)

Table 9. (Concluded).

Group and Definition	Common name	Scientific name
3. (Continued)	Southern red-backed vole	Clethrionomys gapperi
	Prairie vole	Microtus ochrogaster
	House mouse	Mus musculus
	Norway rat	Rattus norvegicus
	Gray fox	Urocyon cineroargenteus
	Eastern spotted skunk	Spilogale putorius
4. Makes extensive use of wetlands, but range encompasses <10% of region	Water shrew	Sorex palustris
	Long-tailed vole	Microtus longicaudus
	Southern bog lemming	Synaptomys cooperi
	Ermine	Mustela erminea
	Moose	Alces alces

in North Dakota during the 1983-84 to 1985-86 seasons, for an average total of $106,766 (Steve Allen, North Dakota Game and Fish Dept., pers. comm.). Buyers in South Dakota paid a total of $57,669 for 3,238 pelts during the 1986-87 season (Larry Fredrickson, South Dakota Game, Fish and Parks, pers. comm.).

The muskrat is the only native mammal that still has a great impact on wetland ecology in the region. Semipermanent wetlands are the most important habitat for muskrat in the region because these basins are abundant, deep enough to sustain under-ice activity in winter, and support growth of emergent plants, especially Typha spp. and Scirpus spp., which provide both food and house-building materials. Muskrats also dig burrows in the banks of wetlands.

Consumption of hydrophytes by high muskrat populations often causes great changes in the interspersion of cover and open water in prairie wetlands. Fritzell states that muskrat densities >50/ha are not unusual. Errington (1948) recorded maximum winter populations of 86 muskrats/ha on a fertile Iowa marsh.

In the extreme southeastern portion of the Dakota pothole region, the importance of muskrat activity on marsh ecology is great. The milder winter climate and more stable water levels there are similar to conditions in Iowa, where high muskrat populations can decimate nearly all emergent hydrophytes and result in mass migration and high mortality, as well as greatly affecting the use of the wetland by other animal species. Here, as semipermanent wetlands cycle between extreme dryness and high water levels, muskrat activity greatly influences nearly all aspects of marsh ecology (Weller and Spatcher 1965; Weller and Fredrickson 1974; van der Valk and Davis 1978a). Van der Valk and Davis (1978a) recognize four stages in this cycle: dry marsh, regenerating marsh, degenerating marsh, and lake marsh (Appendix A, Figure 12). The food and cover requirements of expanding muskrat populations is thought to be an important factor contributing to the decline in emergent hydrophytes that marks the end of the regenerating-marsh phase. If high water levels continue, muskrat populations increase until emergent plants are almost totally destroyed. This leads to the lake-marsh phase, where submersed macrophytes dominate and muskrats are forced to emigrate or suffer high mortality (Errington et al. 1963). The lake-marsh stage will persist until water levels again decline.

The effects of muskrats on the ecology of semipermanent wetlands become much less pronounced in North Dakota, where colder winter climates prevail and wetlands often freeze to the bottom, especially when fall water levels are below average. Under such conditions, foraging is curtailed and populations can be decimated (Seabloom and Beer 1963). Because of increased frequency of drought, muskrat populations in the more arid western portion of the region also do not usually build to levels high enough to greatly diminish emergent vegetation.

Muskrats are an economically important furbearer in the region. Buyer surveys show an average of 64,181 pelts sold in North Dakota during the 1983-84 to 1985-86 trapping seasons, for an average annual return of $103,331 to the takers (Steve Allen, North Dakota Game and Fish Dept., pers. comm.). The harvest in South Dakota averaged about 55,000 during the 1982-83 and 1983-84 seasons (Linscombe and Satterthwaite in press), but better water conditions during the 1986-87 season resulted in sales of 248,126 pelts, for which in-state buyers paid a total of $617,834 (Larry Fredrickson, South Dakota Game, Fish and Parks, pers. comm.).

The mink is common throughout the Prairie Pothole Region and is closely associated with basin wetlands. No reliable census techniques have been developed for this solitary, primarily nocturnal or crepuscular species (A.B. Sargeant, Northern Prairie Wildlife Research Center, pers. comm.). Data from Errington (1943), however, suggest that when surface water is present about 50 ha of semipermanent wetland will support a female with young. Mink populations probably fluctuate greatly in the Prairie Pothole Region in response to drought (Adams 1962; Eberhardt 1974; Fritzell 1989).

Dens are usually located in abandoned muskrat burrows along wetland shorelines (Schadweiler and Storm 1969; Eberhardt 1973; Sargeant et al. 1973; Eberhardt and Sargeant 1977). Females with young in dens can concentrate their activity in relatively small (<20 ha) semipermanent wetlands (Sargeant et al. 1973; Eberhardt and Sargeant 1977) whereas the home ranges of males average 646 ha from May through July and include as many as 30 temporary, seasonal, semipermanent, and permanent wetlands, at least in the Prairie Pothole Region of Manitoba (Arnold 1986).

The concentration of nesting birds in prairie wetlands and the relative scarcity of fish, semiaquatic mammals, and large invertebrates, such as crayfish, in these habitats result in levels of mink predation that can cause significant mortality of marsh birds. For example, Eberhardt and Sargeant (1977) found that on a semipermanent North Dakota wetland, a single mink family can kill 8% of the adult and 52% of the juvenile coots and 20% of the adult and 6% of the juvenile pied-billed grebes. They also found an average of 6.3 adult and 5.3 juvenile ducks taken per mink family, and noted that the preponderance of female diving ducks taken could account for the disparate proportion of males commonly observed among this group of waterfowl. Arnold and Fritzell (1987a, b) estimated that avian prey comprised 55%-75% of the volume of the May-July food of male mink in prairie wetlands in Manitoba.

Economically, mink are a moderately important furbearer in the Dakotas. An average of 4,571 animals were sold to North Dakota buyers during the 1983-84 to 1985-86 seasons, for an average return of $64,497 (Steve Allen, North Dakota Game and Fish Dept., pers. comm.). About 6,000-10,000 mink are estimated to be harvested annually in South Dakota (Linscombe and Satterthwaite in press). During the 1986-87 season, 8,557 pelts were sold to South Dakota buyers, for a return to takers of $203,828 (Larry Fredrickson, South Dakota Game, Fish and Parks, pers. comm.).

The remaining mammals discussed in this report (Group 2 of Table 9) range across at least 10% of the pothole region of the Dakotas, and either regularly make extensive use of prairie wetlands, often during the winter months, or likely can complete their life-cycle in moist, often shrubby, meadows.

Little is known about the life histories of the arctic, masked, and pygmy shrews in the grassland biome, except that marshes or moist habitats, often dominated by cattails or hydrophytic grasses, are used by these tiny carnivores (Jones et al. 1983). Of the three, the arctic shrew seems to be the most wetland oriented, as aquatic invertebrates are a known food item. However, a recent study in the Prairie Pothole Region of north-central South Dakota indicated that pygmy shrews are more abundant than arctic shrews in shallow-marsh zones (Gruebele and Steuter 1988).

The eastern cottontail is primarily a dweller in thickets and brushlands, and the dense stands of willow (Salix spp.) that are sometimes found in wet-meadow zones of prairie wetlands provide permanent habitat. This cottontail is mostly herbivorous, but in times of food shortage may eat mollusks and even carcasses of other cottontails. (Jones et al. 1983). The presence of cottontails around some prairie wetlands is undoubtedly a prime attractant to mustelid and canid carnivores.

The range of the snowshoe hare encompasses roughly the northern half of North Dakota. This hare can be found in wetland wet-meadow zones dominated by willow or aspen (Populus tremuloides). Jones et al. (1983) stated that alder (Alnus spp.) swamps and burned areas with woody regrowth are especially favored. Snowshoe hares are herbivorous, but occasionally eat carrion.

The western harvest mouse ranges throughout the southern two-thirds of the region. Jones et al. (1983) list cattail as a typical habitat and state that the species often associates with meadow voles and uses their runways. Seeds and small amounts of insects are the main food of this small rodent, which is active year around. Up to 18% of the small mammals trapped in South Dakota wetlands by Pendleton (1984) were western harvest mice.

Meadow voles are common herbivores throughout the region, where they inhabit surface runways and tussocks in stands of grasses, sedges, and rushes found in wet-meadow zones (Jones et al. 1983). Cycles of abundance are very pronounced for this species, and population densities as low as 2.5/ha and as high as 617/ha have been reported (Jones et al. 1983). Up to 75% of the small mammals trapped in North Dakota wetlands by Eberhardt (1974) were meadow voles.

This vole is prominent in the diet of the coyote, red fox, mink, long-tailed and least weasels, great horned owl (Bubo virginianus), short-eared owl (Asio flammeus), and northern harrier. The cyclical abundance of voles can greatly affect the seasonal abundance of some of their avian predators.

The meadow jumping mouse occurs throughout the pothole region of the

Dakotas, but the western jumping mouse is mostly restricted to the North Dakota portion (Jones et al. 1983). Both species are mostly found in tall, lush herbaceous or graminoid cover typical of low prairies or wet meadows in the northern plains. Adequate ground cover is essential for nests. Both species are active about 5 months of the year in this area. Material cited in Fritzell (1989) shows that up to 17% of the small mammals trapped in North Dakota wetlands were meadow jumping mice.

The coyote is now the largest common carnivore in the Prairie Pothole Region of the Dakotas and occurs throughout the area, but is most numerous in the western part. Territories for coyote families in south-central North Dakota averaged 61.2 km^2 (Sargeant et al. 1987). Although primarily terrestrial, the coyote hunts in peripheral wetland zones when surface water is present in interior zones, and uses dry and ice-covered wetlands for hunting, traveling, and resting. It also feeds on prey associated with wetlands at various times of the year, including insects, birds and their eggs, cottontails, small rodents, muskrats, beaver, and deer (A.B. Sargeant, Northern Prairie Wildlife Research Center, unpubl. data).

Coyotes are an important furbearer in the region. During the 1983-84 to 1985-86 seasons, North Dakota buyers purchased an average of 7,913 pelts annually, for an average annual combined return to takers of $255,458 (Steve Allen, North Dakota Game and Fish Dept., pers. comm.). In 1986-87, South Dakota buyers purchased 8,149 pelts for a total of $349,674 to takers (Larry Fredrickson, South Dakota Game, Fish and Parks Dept., pers. comm.).

The red fox is common in both Dakotas, and, like the coyote, is primarily a terrestrial species that uses only the shorelines of wetlands when surface water is present, but hunts, travels through, and rests in wetlands when they are dry or ice covered. Territories of red fox families sympatric with coyotes in south-central North Dakota averaged 11.9 km^2 (Sargeant et al. 1987).

Red fox eat a huge variety of foods, mostly animal matter. Foods eaten depend on season and habitat. Common foods found in or at the edges of prairie wetlands include cottontails, meadow voles, harvest mice, jumping mice, young raccoons, and birds and their eggs.

Perhaps the most significant role of the red fox in the ecology of prairie wetlands is as a predator of upland-nesting waterfowl and other semiaquatic birds. Sargeant et al. (1984) estimated the average annual take of adult ducks (both killed and scavenged) by the red fox in midcontinental North America at about 900,000. This impact was greatest in the high-density wetland area of the Missouri Coteau in North Dakota, where a 5-year average of 17.0% of the total prey biomass consumed by foxes during the annual denning season was dabbling ducks.

The red fox has recently been an economically important furbearer in the Prairie Pothole Region, although current (1987) pelt prices are relatively low. During a recent 10-year period (1970-1980), annual harvest in the pothole region of North Dakota alone was 10,000-62,000 pelts that returned $59,000-$2,389,000 to takers (Sargeant et al. 1984). Buyer surveys conducted by Larry Fredrickson (South Dakota Game, Fish and Parks Dept., pers. comm.) indicate that the 17,512 animals purchased there during 1986-87 returned a total of $368,102 to takers.

Before settlement of the Prairie Pothole Region by European man, the omnivorous raccoon inhabited only wooded river valleys in the pothole region of the Dakotas, with greatest densities found in drainages in the eastern part of the region. However, populations expanded greatly after settlement, and raccoons can currently be found throughout the region. Cowan (1973) and Fritzell (1978) found spring raccoon densities of 0.5-3.2 individuals/km^2 in various parts of the region. These studies also showed that wetlands, particularly the seasonal (Class 3) and semipermanent (Class 4) basins of Stewart and Kantrud (1971) were commonly used habitat.

Fritzell (1978) found that raccoon use of wetlands increased greatly from spring to summer as foods become available in these habitats. Greenwood (1982) found that 94% of the nocturnal raccoon activity in eastern North Dakota wetlands was related to foraging, and that the most important food items gathered in these habitats were aquatic insects, birds, bird eggs, snails, and crustaceans.

During the day, raccoons in the pothole region rest, and are seldom found in the same locations on consecutive days from April to July. Use of wetlands for resting sites increases greatly during this period, and by July, 70% of the sites can be located there (Schneider et al. 1971; Cowan 1973; Fritzell 1978).

Raccoons in the northern portions of the Prairie Pothole Region probably do not use wetlands as sites for winter dens, but wintering animals have used dense cattail "teepees" in South Dakota (Fritzell 1989).

The expansion of raccoon populations in the prairie region has been associated with decreased waterfowl nesting success over the past 40 years (Kiel et al. 1972; Duebbert and Kantrud 1974; Trauger and Stoudt 1974; Duebbert and Lokemoen 1976; Sargeant and Arnold 1984). Raccoons feed extensively on waterfowl eggs, especially those of the overwater-nesting diving ducks (Cowan 1973; Greenwood 1981, 1982). Although the total negative impact of this predation on waterfowl populations remains to be determined, it will likely increase as the wetland habitat base continues to decline (Fritzell 1989).

The raccoon has recently become an important fur resource in the pothole region. During the 1983-84 to 1985-86 North Dakota trapping seasons, takers sold an average of 15,881 pelts annually in the state, for which buyers paid a total of $202,006 (Steve Allen, North Dakota Game and Fish Dept. pers. comm.). Recent (1986-87) sales of 34,038 pelts to in-state buyers in South Dakota resulted in a total return of $715,138 to takers (Larry Fredrickson, South Dakota Game, Fish and Parks Dept., pers. comm.).

Few ecological data are available for least and long-tailed weasels in the Prairie Pothole Region. Both species range throughout the region. Weasels prey mostly on voles in this area, and the wet-meadow zones of wetlands are important vole habitat. The long-tailed weasel is a known predator of waterfowl eggs (Keith 1961; Teer 1964), but the likely impact of this mammal on waterfowl is small.

Weasels are unimportant as a fur resource in both Dakotas. Reported annual sales to buyers in both states in the mid-1980's was <100 animals, with prices paid to takers averaging <$0.90/animal (Steve Allen, North Dakota Game and Fish Dep., pers. comm.; Larry Fredrickson, South Dakota Game, Fish and Parks Dept., pers. comm.).

The Prairie Pothole Region lies near the center of the range of the striped skunk. This primarily nocturnal mammal is a ubiquitous predator often associated with wetlands. Densities in the prairie region have varied from 0.4 to 3.1 animals/km^2 (Scott and Selko 1939; Upham 1967; Bjorge et al. 1981; Greenwood et al. 1985).

Literature reviewed by Fritzell indicates that skunks are active in the Prairie Pothole Region from January to November. Eight of twelve winter dens in a large Manitoba marsh were in stands of Phragmites australis (Mutch 1977). Daytime rest areas can be underground or aboveground in dense grasses in uplands or aboveground in stands of emergent hydrophytes in portions of wetlands where surface water is not present.

Striped skunks in the Prairie Pothole Region feed largely on insects during the warmer months, although mice, frogs, birds, shrews, bird and turtle eggs, berries, fruit, worms, and spiders are eaten (Jones et al. 1983). Skunks are major predators of clutches of eggs of upland nesting dabbling ducks (Stoudt 1971; Duebbert and Kantrud 1974; Duebbert and Lokemoen 1980), including many that are likely encountered incidentally as skunks search grasslands for insect prey (A.B. Sargeant, Northern Prairie Wildlife Research Center, pers. comm.). Skunks can also destroy overwater nests of diving ducks if drought conditions increase nest accessibility (Stoudt 1982).

The striped skunk is unimportant economically as a furbearer in both Dakotas. North Dakota dealers reported a total purchase of <200 animals/yr during the 1983-84 to 1985-86 seasons. Takers received an average of only $2.40 each for these pelts (Steve Allen, North Dakota Game and Fish Dept., pers. comm.). Total purchase by South Dakota dealers was 1,878 animals during the 1986-87 season; these pelts returned an average of $2.22 each to takers (Larry Fredrickson, South Dakota Game, Fish and Parks, pers. comm.).

Few quantitative data are available, but anyone who has observed or hunted white-tailed deer in the Prairie Pothole Region is aware of the importance of basin wetlands to this species, especially during the fall and winter. The primary functions of these wetlands are to provide refuge and thermal cover, although some browse (Populus spp. and Salix spp.) and forage (Sonchus spp. and Cirsium spp.) are also obtained (Sparrowe and Springer 1970; Kucera 1976; Fritzell 1989). In North Dakota, dry wetlands are also used as fawning sites (Harmoning 1976).

Dense stands of Typha spp., Scirpus spp., Phragmites australis, and Salix spp. seem to provide the most attractive cover for white-tailed deer in wetlands in this area (H.A. Kantrud pers. obs.). These plants are mostly found in semipermanent wetlands.

White-tailed deer populations have expanded greatly in the Prairie Pothole Region in the last 20 years, likely because of a combination of better management and law enforcement and the great increase in area planted to row crops (corn, sorghum, and sunflower) that provide cover and high-energy winter foods.

The white-tailed deer is an important game species in both states. Latest available estimates place the 1986 harvest in the pothole region of North Dakota at 42,085 (Jim McKenzie, North Dakota Game and Fish Dept., pers. comm.). An estimated 30,424 animals were harvested in 1986 from the area of South Dakota east of the Missouri River (Les Rice, South Dakota Game, Fish and Parks, pers. comm.). Estimates of annual cash flow associated with white-tailed deer hunting in the United States indicate that a single animal is worth $1,657 (Williamson and Doster 1981). Although this figure is undoubtedly high for the Dakotas, it suggests that the income generated to state and local economies by sport hunting of this species is significant.

Summary

Fritzell (1989) summarized the role of wetlands in the life cycle of mammals in the Prairie Pothole

Region. He concluded that these habitats are of direct importance to many species, and that some mammals markedly affect other components of wetland ecosystems and the values humans extract from them. He cited in particular the effects of the muskrat on nutrient exchange and vegetative structure in wetlands and the importance of wetlands in predator-prey relationships that can significantly affect the production of waterfowl and other wetland wildlife. He also noted that the harvest of furbearers and white-tailed deer in prairie wetlands is an important contribution to local economies.

CHAPTER 4. ECOLOGICAL PROCESSES

4.1 PHYSICAL FUNCTIONS

The two main physical functions of prairie wetlands are their hydrologic and water quality effects. Although strongly interrelated, these functions will be discussed separately in this section. Descriptive material on hydrology and water quality is found in Sections 2.3 and 2.4, respectively.

Hydrologic Functions

The hydrology of prairie wetlands is known only superficially, even though it has been obvious for decades that this knowledge is crucial if the conflicts between agricultural water users and those concerned with flood protection, water quality, ground-water recharge, and fish and wildlife production are to be resolved (Winter 1988). The basin wetlands that are the subject of this community profile form the core of these conflicting interests.

The value of prairie basin wetlands as retainers of surface water flows has recently been reviewed by Winter (1989). He states that, before drainage, the numerous small depressions that characterize the topography made much of the region non-contributary to surface runoff until depressions were full of water and began to overflow from one to the next. In addition, when overflow did occur, the extremely low regional gradient of the land surface generally made runoff velocities small.

Although the number of runoff-retaining basins in the Prairie Pothole Region of the Dakotas was large and much drainage has been completed, controversy as to the proven effects of wetland drainage as a cause of increased flooding continues. Several completed studies have been criticized, largely because of problems of study design and impacts of conditions antecedent to the studies (Winter 1988). Even so, the results of some of these studies will be reported here.

Ludden et al. (1983) in the Devils Lake basin of North Dakota concluded that depressions can store as much as 72% of total runoff in a 2-year-frequency runoff event and 41% of total runoff from a 100-year-frequency runoff event, with a maximum storage capacity of nearly 8×10^8 m^3 available. In an undrained control block in North Dakota's J. Clark Salyer National Wildlife Refuge, all local runoff plus 58% of the inflow was retained in wetlands (Malcolm 1979).

Increased streamflows in the southern Red River Valley in North Dakota were strongly correlated to the increase in area artificially drained in each drainage basin (Brun et al. 1981), and wetlands in the Red River system significantly reduced flood levels downstream in major metropolitan areas (Jahn 1981).

A little-understood function of prairie wetlands is their role in regional ground-water recharge and discharge (Winter 1989). Considerably more work needs to be done on this subject, especially on water-flow rates through strata of various glacial deposits. Of eight hydrological studies of palustrine and lacustrine wetland systems conducted in the glaciated prairies of North America, seven showed that these wetlands contributed to ground-water recharge (Adamus and Stockwell 1983). The eighth study showed that wetlands with permanently flooded water regimes contributed ground-water discharge year-round. Preliminary studies indicate that basin wetlands in North Dakota supply water to discharge sites up to 20 km distant (Swanson et al. 1988).

Water Quality Functions

It was shown in Section 2.4 that prairie wetlands naturally vary greatly in the chemical composition of their surface waters. This is only one aspect of "quality." The quality of water depends on what the water is to be used for. The human users of water found in prairie wetlands include cities, households, ranches, and crop irrigators, who usually desire water low in dissolved minerals or organic compounds, as well as commercial chemical companies, who extract usable minerals most effectively from some of the most saline surface waters found in the region. Other users desire water of low temperature or low in suspended material. For purposes of this section, water of highest quality is considered that unchanged from its original chemical composition under pristine conditions.

Of the 11 biological and nonbiological functions of wetlands listed by Adamus and Stockwell (1983), sediment trapping and nutrient removal have the greatest positive impact on water quality. These two functions have recently been reviewed for prairie wetlands by Neely and Baker (1989), and this section will draw heavily from their findings.

Most prairie wetlands that have escaped drainage now lie in watersheds devoted primarily to agricultural crop production. Hence, these wetlands frequently experience large inputs of sediment, fertilizer, and other agricultural chemicals transported in sediment, surface runoff water, and subsurface drainage. These contaminants are often removed from the water in passing through wetland basins. Prairie wetlands can thus be important in preservation of local water quality.

Contaminants transported mainly with sediment include chlorinated hydrocarbon insecticides; herbicides such as trifluralin, profluralin, and paraquat; and total organic N and total P including phosphate. Ammonium nitrogen and a majority of the pesticides used in the midwestern United States are carried to wetlands mostly with surface water runoff. Nitrate nitrogen is the most important chemical carried by subsurface drainage, and can be transported mostly by surface drainage in relatively impervious or wet soils. Grue et al. (1988) demonstrated that aerial application of methyl and ethyl parathion caused mortality on aquatic invertebrates for up to 18 days after spraying.

Only the role of prairie wetlands as sinks or traps for N and P has been studied to any great extent, and most of the information comes from studies of a single Iowa wetland (Davis and van der Valk 1978; Davis et al. 1981; Neely 1982). These nutrients can be transferred from the water column of wetlands to the atmosphere, to the interstitial water of sediments, or to biomass within the wetland. Each of these compartments can also return nutrients to the water column.

The Iowa wetland mentioned above removed 86% of the NO_3^- nitrogen, 78% of the NH_4^+ nitrogen, and 20% of the PO_4^{3+} phosphorus inputs from agricultural runoff in a single year, but the wetland showed such high efficiency as a nutrient trap only when no outflow occurred. Nevertheless, sequential processes of nitrification and denitrification can result in large N losses to the atmosphere, to surface outflow, and to the ground-water system in wetlands experiencing frequent drying and inundation. Thus it would seem that temporarily and seasonally flooded prairie wetlands would be especially efficient in removal of excess N that entered their basins.

Investigators of the Iowa wetland referred to above also reported high N and P concentrations in tissues of the two most common emergent plants, Typha glauca and Sparganium eurycarpum. If it is assumed that other emergents also accumulate these nutrients, then the removal of hay and forage from prairie wetlands by humans and their livestock would be a means by which their function as nutrient traps could be maintained for longer periods.

Many prairie wetlands likely retain sediment, nutrients, and other anthropogenic substances simply because the basins have no outlet. No studies have addressed the ability of these wetlands to withstand sustained inputs of these contaminants. In addition, no study has addressed the question of the fate of nutrients and pesticides that enter highly saline prairie wetlands.

4.2 BIOLOGICAL FUNCTIONS

Primary production, which links inorganic resources (energy and nutrients) to food-chain support and associated secondary production, is certainly the most important biological function of all ecosystems, and is the foundation for most human use of these ecosystems. The basis for food-chain support in prairie wetlands has recently been reviewed by Murkin (1989), and this section will draw heavily on his work.

The heterotrophic primary consumers in prairie wetlands consist of herbivores and detritivores. Invertebrates, muskrats, and waterfowl are important herbivores in prairie wetlands. A large group of invertebrates are known to ingest living phytoplankton and attached algae, but little is known of the role of algae in the support of these primary consumers in prairie wetlands. Some of the most important of these herbivores in prairie wetlands include macro- and microcrustaceans, dipteran and ephemeropteran insects, and freshwater mollusks. Domestic animals also consume much of the primary production from prairie wetlands, but are unimportant in many other of the world's wetland ecosystems. At least one emergent hydrophyte, Scolochloa festucacea, is recognized as a highly valuable livestock forage grass and is actively managed for and harvested in prairie wetlands (Neckles et al. 1985).

Secondary consumers are extremely important and provide foods for most of the higher organisms found in prairie wetlands. Murkin stated that knowledge of the basic ecology and life-history of consumers in prairie wetlands is so limited as to make work on secondary production impossible at this time.

A third, nontrophic user of primary production is the large and diverse group of organisms that depend on living and dead plants for thermal cover, nesting material, sites for egg attachment, etc. These organisms will not be discussed here, but some information on nontrophic use is presented in the preceding chapters on various animal groups.

Primary Production

Net primary production, both above and below ground level, is particularly high in prairie wetlands (van der Valk and Davis 1978b), but shows great temporal variation, mainly because of the presence or absence of surface water; water levels are also important in this regard. In semipermanent wetlands, highest primary productivity likely occurs as emergent hydrophytes regenerate when surface water is replenished after prolonged drought, and lowest productivity probably occurs after several years of high water levels when emergent hydrophytes are replaced by submersed species (van der Valk and Davis 1978a). In temporary and seasonal wetland basins, productivity likely is highest when water is present, as judged by increases in height, biomass, and density of emergent macrophytes (Neckles 1984; H.A. Kantrud, pers. obs.).

Examples of production rates and above- and below-ground biomass for various vegetation zones and some common species in prairie wetlands are shown in Table 10. In many instances, algae do not contribute greatly to standing-crop biomass, and thus are not usually considered an important part of primary production. However, recent investigations by Hooper and Robinson (1976) and Shamess et al. (1985), and unpublished data of van der Valk (Murkin 1989), show that algal production and biomass in prairie wetlands can be quite high (Table 10). Algal groups especially important as primary producers in prairie wetlands are epiphytes, which grow on surfaces of submersed plant material; epipelics, which grow on bottom substrates; and metaphytes, which usually form floating mats. Prairie wetlands can produce high

Table 10. Examples of biomass and production rates of some primary producers in prairie wetlands (modified from Murkin 1989).

Primary producer	Biomass or production rate (g/m^2 dry wt.) or ($gC/m^2/yr$)	Reference
Vascular hydrophytes		
Above ground biomass		
Wet-meadow zones	306	Barker and Fulton (1979)
Shallow-marsh zones	525	
Deep-marsh zones		
emergent	968	"
submergent	551	"
Typha glauca	2106	van der Valk and Davis 1978b
Scirpus validus	602	
Scolochloa festucacea (dry zone)	80	Neckles 1984
" " (wet zone)	110	"
Potamogeton pectinatus	250	Anderson 1978
Below ground biomass		
Typha glauca	1442	van der Valk and Davis 1978b
Scirpus acutus	1870	
Phragmites australis	1565	"
Algae		
Metaphytic (biomass)	268	van der Valk (unpubl.)
Epiphytic (production rate)	48.5	Hooper and Robinson 1976
Epipelic (production rate)	300	Robinson pers. comm. cited in Murkin (1989)

midsummer populations of planktonic algae of sufficient density to cause fish kills (Kling 1975).

Virtually nothing is known about the most primitive producer group in prairie wetlands, the chemosynthetic bacteria.

Decomposition

There is no doubt that huge herds of wild ungulates once removed considerable amounts of primary production from prairie wetlands. This phenomenon has been continued on many wetlands through man's livestock and hay-cutting operations. Birds (primarily waterfowl) are also known to consume up to 86.8 gm/m^2 vegetative biomass annually from portions of certain prairie wetlands (Anderson and Low 1976). The emergence of aquatic flying insects may also remove significant primary production, although not enough is known about the foods of larval insects to quantify this relationship. However, as many as 19,713 adult chironomids/m^2 have been trapped in a single month as they emerged from a semipermanent North Dakota wetland (Nelson and Butler 1987). Nevertheless, the generally high productivity of most prairie wetlands ensures that a considerable amount of material enters the system as detritus.

An important part of the detritus pool in prairie wetlands is standing dead emergent hydrophytes. Much of this litter enters the pool with the onset of killing frosts at the end of the growing season, but in less permanent wetlands, many emergent hydrophytes die from drought during late summer and early fall. Leaf and shoot death of various emergent species can occur at any time during the growing season (van der Valk and Davis 1978b).

The fallen litter compartment is usually considered to consist of material in the water column, including fallen or bent-over stems and leaves of emergents, submersed macrophytes, and algae. Some living emergent material can enter this compartment directly through muskrat activities (van der Valk and Davis 1978b) or those of man and his livestock. The third component of the detritus pool is the dissolved organic substances that leach into the water column from both standing and fallen litter.

De la Cruz (1979) recognized three simultaneous processes whereby detritus is decomposed: (1) rapid leaching of soluble substances from newly dead plant tissue, (2) weathering and mechanical fragmentation, and (3) biological decay from bacteria and fungi. Particle sizes rapidly decrease, and the dead tissue and soluble organic substances become food for a host of invertebrates and other life forms whose excretory products can again be colonized by microbes.

Detritivory

There is no doubt that detritivory is an important aspect of food chain support in prairie wetlands, even though there are no estimates of detrital consumption and utilization for any wetlands. Coarse particulate matter likely enters prairie wetlands as a pulse associated with increased spring water temperatures. Bacteria, fungi, and other microorganisms form the first level of consumption of dead plant material and are considered the base of the detrital food chain, with secondary production assumed to occur at higher trophic levels. Many of the invertebrate herbivores common to prairie wetlands are also suspected to be detritivores, but some authors argue that such organisms may simply be assimilating microorganisms associated with litter of small particle size. Thus Murkin (1989) concluded that the primary role of detritus in prairie wetlands may be to provide habitat necessary for algae and invertebrate production in these systems.

CHAPTER 5. HUMAN USES AND IMPACTS

5.1 ECONOMIC FUNCTIONS

The natural wetlands of North and South Dakota supply important economic and recreational benefits to the nation as a result of their prominence in the production of waterfowl and other migratory birds. Among the most important local, state, and regional benefits are providing water and forage to livestock, offering extensive recreational opportunities through hunting and fishing, flood control, ground-water recharge, and improving water quality. The importance of wetland habitat for wildlife, recreation, aesthetic values, and water quality is recognized by 9 out of 10 North Dakotans, based upon a recent poll (Fargo Forum, 31 December 1986; North Dakota Bureau of Governmental Affairs, unpubl. data). The same poll indicated 77% of the State's residents want tougher enforcement of laws controlling wetland drainage. Yet wetland protection is a politically contentious issue because grain growers, a dominant sector in the economy of most communities, cannot capture payment for many of the values society derives from wetlands. As a result, free-market incentives to drain are often stronger than those to maintain wetland habitat (Leitch 1983) and efforts to protect wetland habitat are often resisted. Drainage has also been encouraged because Federal price supports on agricultural commodities are paid equally whether crops are grown in the uplands or in drained wetland basins. The U.S. Congress addressed this issue in the Food Security Act of 1985 (Farm Bill) (H.R. 2100) by making agricultural producers ineligible for certain Federal assistance if they alter or drain wetlands existing after 23 December 1985, and produce agricultural commodities on these converted lands.

No economic benefits derived from prairie wetlands are more widely disseminated than those resulting from waterfowl production. The North American waterfowl resource, particularly the forms produced in prairie wetlands, contribute significant economic benefits to most states and numerous local communities. At the national level, waterfowl, including those produced in prairie wetlands, support recreation for about 2 million waterfowl hunters (Novara et al. 1987). An estimated $638 million was spent on migratory bird hunting in the United States in 1980 and an estimated $6.6 billion is spent annually for recreation related to nongame wildlife (U.S. Department of the Interior 1982). A significant part of both expenditures results from migratory birds reared in prairie wetlands.

In North and South Dakota, waterfowl hunting is a major recreational activity; the former state ranks first in the nation in number of waterfowl hunters per capita. Also, several thousand nonresidents travel to each of these states to hunt waterfowl each year and contribute several million dollars to local economies. In South Dakota, recreation associated with hunting the ring-necked pheasant brings $35 million annually to the State (U.S. Department of the Interior, Fish and Wildlife Service 1987), and is a significant source of income to many rural communities. Pheasants rely on wetlands for a major part of their winter habitat requirements in the Prairie Pothole Region. Trapping and hunting of resident furbearers provides a supplemental income source to several thousand residents of the Dakotas. Highly valued furbearers including the mink, muskrat, and raccoon occur primarily in association with prairie wetlands (See Section 3.7).

5.2 WETLAND OWNERSHIP

Wetlands in the Dakotas are primarily in private ownership, with significant holdings by Federal and State agencies. The primary public landholders managing lands for wildlife production are the U.S. Fish and Wildlife Service (FWS); the South Dakota Department of Game, Fish and Parks; and the North Dakota Game and Fish Department. Private trusts and local and national conservation organizations own and manage some wetland tracts for wildlife production in both states. Of an estimated 810,000 ha and 526,500 ha of natural wetland habitat existing in North and South Dakota, respectively, less than 10% is owned in fee title by public and private wildlife interests. The principal public agency owning wetlands, FWS, has fee title to about 36,000 and 17,000 ha of wetlands in waterfowl production areas in the Prairie Pothole Region of North and South Dakota, respectively (Krapu and Duebbert 1989). There are also several thousand hectares of wetland habitat on National Wildlife Refuges (NWR's) in these states. In addition, as of September 30, 1988, perpetual easements have been taken by FWS on 313,352 and 158,057 ha of privately owned wetlands in North and South Dakota, respectively (U.S. Department of Interior unpubl.). These easements protect contracted wetlands in perpetuity from draining, burning, or filling by the landowner or operator, but the land can be tilled, grazed, or hayed when natural conditions permit.

State conservation agencies in North and South Dakota own approximately 9,300 and 21,870 ha of natural wetlands, respectively (Krapu and Duebbert 1989). A significant but uninventoried area of wetlands is contained in the unpatented State-owned lands lying below the meander line of natural lakes and on State-owned school lands (Morgan 1971). Meandered wetlands are mostly permanent or intermittent alkali lakes. An estimated 64,655 ha of meandered wetlands exist in South Dakota (Wittmier 1982); similar statistics are not available for North Dakota. Lands granted to the State for the support of public schools include a wide array of wetland types, including highly productive waterfowl habitat, and are located primarily within native grassland pastures leased for grazing. A total of 152,720 and 62,147 ha of State school lands of all habitat types remain in public ownership in the Prairie Pothole Region of North and South Dakota, respectively (State of North Dakota, Commissioner of University and School Lands 1987; South Dakota Office of School and Public Lands 1987). State school lands are not protected from eventual sale and over three-quarters have been sold in North and South Dakota. The current policy in North Dakota is to maintain remaining school lands in state ownership, whereas South Dakota is continuing to sell its school lands (South Dakota Office of School and Public Lands 1987). A small amount of wetland habitat is located on lands administered by other State agencies, e.g., in state parks and state forests. Other Federal agencies owning limited natural wetland habitat in the Prairie Pothole Region of the Dakotas include the Forest Service, Bureau of Reclamation, Army Corps of Engineers, Bureau of Land Management, Bureau of Indian Affairs, and Department of Defense.

5.3 WETLAND DEGRADATION AND DRAINAGE

Artificial drainage and degradation of wetland habitat represent major threats to breeding populations of waterfowl and other marsh birds in the Prairie Pothole Region. It is estimated that approximately 60% and 40% of the original wetland area has been drained in North Dakota and South Dakota, respectively (Tiner 1984). Nearly all agricultural wetland drainage in the Dakotas has been by surface ditches, although underground tiles have been used to a small extent, mostly in the southeastern part of the region. Agricultural wetland drainage is often closely linked to highway construction projects that provide the conduit for waters drained from fields (U.S. Fish and Wildl. Serv. 1975). Some wetland basins no longer hold water because of the effects of drainage on shallow aquifers that recharge them, while the waters of a few basins are pumped or siphoned off during the spring. Winter (1989) warned that the problems associated with modification of local hydrologic systems are self-perpetuating and that multiple modifications can ultimately lead to regional impacts.

Systematic sampling of wetland drainage in South Dakota by the U.S. Fish and Wildlife Service for the period 1974-1980 indicated that 4.4% of the area of seasonal and semipermanent wetland basins unprotected at the end of 1974 in the survey areas were destroyed during the period (Memorandum to the Area Manager, Fish and Wildlife Service, Pierre, South Dakota, 17 December 1980). Northeastern portions of the state had relatively low drainage rates (1.5% of area of wetlands destroyed), whereas rates were as high as 7.5% in southeastern South Dakota. Wittmier (1982) estimated that 34,505 ha of temporary, seasonal, and semipermanent basins have been drained in South Dakota since 1964. The latest private drainage survey data for North Dakota (Memorandum to the Area Manager, Fish and Wildlife Service, Bismarck, North Dakota, 29 May 1980) stated that 10.6% of the area of all privately owned natural basin wetlands in the Prairie Pothole Region of the state were drained from 1966 to 1980. The survey did not include temporary basins, so the loss rate is a conservative estimate.

Wetland drainage has been most extensive in the Central Lowlands portion of the Dakotas (Figure 1) (Nelson et al. 1984). Drainage rates vary widely among localities, in part depending on the proportion of the wetland base that is protected by perpetual easements acquired by the U.S. Fish and Wildlife Service under the Small Wetlands Acquisition Program.

The primary cause of wetland degradation in the Prairie Pothole Region, including the part occurring in the Dakotas, is agriculture (Tiner 1984). Intentional filling of basins with soil from adjacent uplands occurs, but is not common. More insidious is the gradual siltation of basins caused by soil erosion from adjacent cropland. This cause of wetland degradation has become more severe in recent years with the advent of larger, more powerful farm equipment that allows cultivation of entire basins and their steeply rolling watersheds. Increased siltation to basins can also be attributed partly to expanded planting of row crops, particularly corn, sunflower, and soybean. Row crops generally result in more soil erosion than small grains, because of the additional cultivation required during the growing season.

Agricultural chemicals exert a subtle but pervasive influence on prairie wetlands. Agricultural chemicals are widely used in association with growing intensification of land use in the Dakotas. Most cropland in the two states is regularly treated with herbicides, but insecticide use is restricted primarily to sunflowers, which are now a widely grown crop; 65% of the sunflower hectarage in North Dakota was treated with insecticides in 1984 (Grue et al. 1988). Widespread aerial application of agricultural chemicals in the Dakotas exposes wetland animal life and plants to overspray and drift. Although more research is needed, preliminary studies in North Dakota indicate that the potential for agricultural chemicals to enter prairie wetlands and influence survival and reproduction of wildlife is high, particularly for the most toxic and widely used insecticides (Grue et al. 1986). The impact of herbicides on prairie wildlife is indirect and comes primarily from elimination of food and cover (Hudson et al. 1984; Hill and Camardese 1986).

If degradation and destruction of waterfowl breeding habitat continues at present rates into the next century, stocks of ducks can be expected to decline accordingly. Therefore, a wide array of measures will be needed to partially circumvent these losses, including increased production of waterfowl on publicly owned lands, restoration of lands that formerly were prime breeding habitat, and slowing further habitat loss.

5.4 WETLAND MANAGEMENT AND RESTORATION

Prairie wetlands are underlain by fertile soils, and under natural conditions, a high proportion undergo annual drawdowns and are inherently productive of the foods that support many species of migratory birds, including waterfowl. However, extensive drainage and degradation of wetlands in the Dakotas has reduced or eliminated a major part of the highly productive temporary and seasonal wetland component in many localities, thereby reducing productivity and making intensive management attractive as a means of enhancing waterfowl habitat. The potential for intensive management of water levels is limited by land topography to a relatively small part of the wetland base; e.g., a few State-owned waterfowl management areas and National Wildlife Refuges. Intensive management of marsh habitat in the Dakotas is increasing, however, due primarily to habitat management efforts by Ducks Unlimited on publicly owned wetlands.

The need for wetland management in the Prairie Pothole Region is not restricted to manipulation of water levels. Elimination of the natural biotic forces of fire and ungulate grazing on many nontilled wetlands decreases insolation of surface waters and rates of nutrient turnover, thereby decreasing productivity of life forms adapted to shallow, open water (see Section 2). Vegetation of shallow waters, if not removed by herbivores or otherwise cropped, often develops into rank and dense stands that discourage use by many aquatic species, including waterfowl. Some form of vegetation manipulation on shallow wetlands is desirable as part of the management of lands to maintain high cover quality for waterfowl production.

Wetland restoration has high potential for increasing productivity of wetland complexes in North and South Dakota that have lost critical wetland habitat through drainage. This management tool is being used with increasing frequency, particularly on lands retired from crop production under 10-year contracts through the Conservation Reserve Program (CRP), on lands deeded back to or on those lands where loans are administered by the Farmers Home Administration (FmHA), and to replace wetland habitat lost during construction of public works projects. With an estimated 1.5 million ha of drained wetlands in the Dakotas, widespread opportunities exist to restore wetlands within the states' cropland base. In conjunction with the CRP, FWS offers participating landowners an additional payment in return for the right to restore wetland habitat in the tract. In North Dakota, the reformulated wildlife mitigation plan for the Garrison Diversion Unit includes planned restoration of 4,499 ha of former wetland as replacements for wetlands lost during project construction (U.S. Department of Interior 1987). The scale of future wetland restoration in North and South Dakota will depend primarily on the direction taken by Federal agricultural programs. With sufficient incentives to agricultural producers, large-scale wetland restoration programs are feasible with major potential benefits to North American waterfowl and other wildlife populations.

5.5 PROSPECTS FOR THE FUTURE

The importance of prairie potholes to North American migratory bird populations is widely recognized (U.S. Department of the Interior and Environment Canada 1986). Recognition of prairie wetland values and the forces contributing to their degradation and destruction has resulted in several remedial actions being taken in recent years. Among the most important has been the incorporation of stringent mitigation measures into Federal water projects in the Dakotas to replace wetland habitat lost during project construction (Krapu and Duebbert 1989). Replacement of wetland habitat lost through restoration on a 1:1 basis with habitat of an ecologically equivalent type, as has been done in the reformulated Garrison Diversion Unit, reflects the growing concern of the Federal Government toward prairie wetland loss and the need for replacement when destruction occurs. Other recent measures of importance to prairie wetland conservation in the Dakotas include the Emergency Wetland Resources Act of 1986 (P.L. 99-645), which assures continued funding of wetlands preservation through migratory waterfowl hunting stamp sales and other means, and the Swampbuster provision of the 1985 Farm Bill (H.R. 2100) which sets substantial monetary penalties for agricultural producers who drain wetlands and plant to annual crops after December 23, 1985. The latter action, a marked departure from past Federal agricultural policies, will, if strictly enforced, add a significant new tool for reducing drainage of prairie wetlands. This law is potentially effective in the Dakotas because most agricultural producers there rely upon Government price supports and other Federal subsidies for a significant part of their annual farm income (Heimlich and Langner 1986).

The greatest challenge to maintaining a productive wetland base in the Dakotas is presented in the Central Lowlands. There, in many locations, an extensive wetland base remains, in part because of perpetual easements obtained by FWS, but much habitat continues to be degraded and/or drained by large cereal-grain farming operations. The Swampbuster provision may help to slow wetland drainage, but additional measures are needed to more fully protect watersheds and provide nesting cover for waterfowl and other wildlife. Expansion of Federal land retirement programs such as Waterbank and the CRP are needed to reduce pressures to drain or degrade wetland habitats. There is also a substantial land base currently in private ownership in the Dakotas that offers limited economic returns to private landowners, but makes or could make a major contribution to national and international migratory bird habitat requirements. The gradual transfer of habitat management rights on a substantial part of these lands through purchase in fee title and/or the taking of conservation easements is essential for the long-term well-being of waterfowl and other migratory birds that are dependent on prairie wetlands during part of their life cycles.

A cooperative agreement between the United States and Canada, the North American Waterfowl Management Plan (U.S. Department of the Interior and Environment Canada 1986), represents the foremost effort currently underway to rebuild North American waterfowl populations. The plan seeks to restore populations to 1970-79 levels.

The plan is continental in scope, with major elements proposed for the Prairie Pothole Region. One goal is to protect and improve 445,000 ha of additional waterfowl habitat in the midcontinent region. A substantial part of that habitat could come from the Dakotas through perpetual easements on wetlands and grasslands and through acquisition in fee title. Other important elements include financial incentives to landowners to manage lands to produce waterfowl and through more intensive management of existing publicly owned lands.

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Appendix A. Algal taxa, maximum densities, and month(s) (in parentheses) of observed maximum density in the water column of selected seasonal and semipermanent wetlands in the Cottonwood Lake study area, Stutsman County, North Dakota, in 1984 (from LaBaugh and Swanson 1988).

	Seasonal wetlands		Semipermanent wetlands		
	T8	T3	P1	P8	P11
Basin chemical type^{a}	$KHCO_3$	$CaSO_4$	$MgSO_4$	$MgHCO_3$	$NaSO_4$
Dominant emergents in central zone	Polygonum coccineum-Carex atherodes	Scolochloa festucacea-Carex atherodes	Typha spp.-Scirpus acutus	Typha spp.-Scirpus acutus	Scirpus maritimus Scirpus acutus
Cyanophyta					
Anabaena sp.	435^{b}(7)		95 (9)	354 (10)	417 (7,8)
A. sp. 1	530 (5)	559 (6)			
A. sp. 2	133 (5)	95 (6)			
A. sp. 3		28 (6)			
A. catenula				189 (10)	
A. planctonica	360 (5)	7356 (5)			
Aphanizomenon sp.					587 (8)
Aphanocapsa sp.	786 (5)				
A. delicatissima	1240 (6)	5640 (6)	473 (6)	3173 (10)	5680 (5)
A. elachista	12969 (7)	511 (6)		909 (7)	3976 (5)
A. pulchra	189 (5)				
Aphanothece sp.	3114 (5)	14844 (6)	3086 (10)	2779 (10)	1060 (6)
A. sp. 1		369 (6)			
A. sp. 2		975 (6)			
A. castagnei	701 (5)				
A. saxicola				2833 (10)	
Borzia sp.		2461 (5)			
B. tricocularis					2253 (8)
Chamaesiphon curvatus			9 (7)		
Chroococcus sp.	102070 (6)	691 (5)	265 (6)	701 (6)	85 (6)
C. sp. 1	77172 (6)		2234 (10)	293 (6)	1325 (6)
C. sp. 2	9 (5)		455 (7)	473 (7)	1477 (7)
C. sp. 3			19 (8)		
C. dispersus	1477 (6)	4951 (6)	133 (10)	2348 (8)	
C. pallidus	6494 (5)				
C. refractus				76 (6)	

(Continued)

Appendix A. (Continued).

Basin chemical type[a] Dominant emergents in central zone	Seasonal wetlands		Semipermanent wetlands		
	T8 $KHCO_3$ *Polygonum coccineum-Carex atherodes*	T3 $CaSO_4$ *Scolochloa festucacea-Carex atherodes*	P1 $MgSO_4$ *Typha* spp.-*Scirpus acutus*	P8 $MgHCO_3$ *Typha* spp.-*Scirpus acutus*	P11 $NaSO_4$ *Scirpus maritimus* *Scirpus acutus*
Coelosphaerium sp.	4279 (7)				
C. collinsii			1742 (5)		
C. dubium		1259 (6)			
Dactylococcopsis sp.		398 (7)			
D. acicularis	9 (5,7)	76 (6)	9 (7)	19 (5)	
D. fascicularis		57 (6)		66 (7)	9656 (5)
D. irregularis				21 (10)	
D. raphidioides			9 (8)		
D. smithii	47 (5)	38 (5)	9 (5)	66 (5)	35074 (5)
Gloeocapsa sp.	133 (6)	5623 (5)		83 (10)	2286 (8)
G. conglomerata				824 (10)	
Gloethece linearis			38 (9)		
Holopedium irregulare	6021 (7)	738 (6)			
Lyngbya sp.		1136 (7)	114 (7)	1083 (10)	8804 (5)
L. limnetica			549 (10)		
L. nana	189 (7)	1704 (7)	701 (5)		
L. vericolor				1583 (10)	
Marssoniella elegans				76 (6)	
Merismopedia minima				21 (10)	76 (8)
M. irregularis				166 (10)	
M. tenuissima					2272 (5)
Microcystis sp.		417 (6)		417 (5)	
M. labens				208 (10)	
Nodularia sp.				540 (9)	
Nostoc sp.				142 (6)	
Oscillatoria sp.	909 (6)	379 (7)	417 (9)	3578 (7)	6958 (5)
O. sp. 1			417 (7)	341 (7)	928 (7)
O. sp. 2			284 (7)	151 (7)	103 (8)
O. agardhii			530 (10)		
O. angusta	189 (7)		776 (10)	795 (8)	2274 (10)

(Continued)

Appendix A. (Continued).

Basin chemical type[a] Dominant emergents in central zone	Seasonal wetlands T8 KHCO$_3$ Polygonum coccineum-Carex atherodes	 T3 CaSO$_4$ Scolochloa festucacea-Carex atherodes	Semipermanent wetlands P1 MgSO$_4$ Typha spp.-Scirpus acutus	 P8 MgHCO$_3$ Typha spp.-Scirpus acutus	 P11 NaSO$_4$ Scirpus maritimus Scirpus acutus
O. angustata		454 (5)			
O. angustissima	2357 (6)	6229 (7)	1774 (10)	1791 (10)	4544 (5,10)
O. chalybea				1583 (10)	
O. chlorina				2000 (10)	12922 (5)
O. limnetica	966 (7)	2083 (7)	1164 (9)	1375 (10)	2021 (10)
O. limosa					3692 (5)
O. minnesotensis					4970 (5)
O. planctonica		568 (7)			
O. princeps	360 (6)		530 (8)	227 (7)	
O. splendida			246 (9)		
Phormidium sp.	120 (6)	76 (5)	379 (10)	114 (5)	8864 (10)
P. foveolarum		492 (5)	1704 (9)	151 (9)	303 (7)
P. fragile					505 (10)
P. laminosum				322 (7)	
P. luridum				341 (6)	
Pleurocapsa sp.				5498 (10)	
P. fuliginosa				542 (10)	
Pseudoanabaena sp.	719 (6)	1022 (5)		1108 (6)	
Raphidiopsis mediterranea				2272 (8)	
R. minima				189 (7)	
Rhabdoderma sp.			19 (9)		76 (8)
R. irregulare	3408 (7)			57 (7)	539 (9)
R. minima			114 (9)	665 (10)	
R. sigmoidea	417 (7)	9788 (6)	3124 (8)	38435 (8)	12922 (5)
R. s. var minor	171 (6)	5831 (7)	360 (10)	1856 (7)	568 (5)
Schizothrix sp.		189 (7)		947 (7)	
S. c. f. arenaria				256 (6)	
Spirulina sp.			57 (10)	180 (8)	
S. sp. 1			57 (9)		
S. sp. 2			19 (10)		

(Continued)

Appendix A. (Continued).

Basin chemical type[a] Dominant emergents in central zone	Seasonal wetlands T8 $KHCO_3$ Polygonum coccineum-Carex atherodes	Seasonal wetlands T3 $CaSO_4$ Scolochloa festucacea-Carex atherodes	Semipermanent wetlands P1 $MgSO_4$ Typha spp.-Scirpus acutus	Semipermanent wetlands P8 $MgHCO_3$ Typha spp.-Scirpus acutus	Semipermanent wetlands P11 $NaSO_4$ Scirpus maritimus Scirpus acutus
S. c. f. okensis		76 (6)			
S. laxa				76 (10)	
S. laxissima			28 (9)	208 (10)	1136 (5)
S. major				292 (10)	63 (10)
S. princeps			9 (9)		6248 (5)
S. tenerrima				166 (10)	
Symplocastrum sp.				333 (10)	
Synechococcus sp.	4552 (7)		1155 (10)	85825 (5)	1314068 (5)
S. sp. 1		795 (5)			929248 (5)
S. sp. 2		2651 (6)			170 (7)
S. aeruginosa	322 (7)	1704 (6)	398 (10)	284 (6)	2272 (5)
S. elongatus	76 (6)	60473 (6)	1155 (10)	473 (6)	568 (5)
S. linearis	5263 (7)	1004 (7)	284 (8)	729 (8)	18318 (5)
S. l. var spirale	208 (6)			151 (8)	189 (10)
S. racemosus				38 (7)	1098 (7)
Synechocystis sp.					104 (7)
S. aquatilis			95 (6)	398 (6)	
Cryptophyta					
Chroomonas sp.	2651 (7)	96 (6)		341 (6)	3342 (7)
C. nordstedtii		57 (5)	2414 (6)	28 (6)	
Cryptomonas sp.			227 (10)		331 (5)
C. sp. 1	909 (5)	38 (5)	19 (5,6,10)	6051 (10)	
C. sp. 2	123 (5)	66 (6)	208 (5)	932 (10)	
C. sp. 3	11814 (7)			132 (10)	
C. sp. 4				4654 (10)	
C. erosa	294 (6)	738 (6)	928 (6)	795 (5)	5 (7)
C. marsonii	47 (7)	38 (6,7)	57 (10)	360 (7)	
C. ovata	57 (6)	76 (6)		5 (8)	
C. rostratoformis	115 (6)		19 (5,10)	132 (5)	
C. truncata					757 (5)

(Continued)

Appendix A. (Continued).

	Seasonal wetlands		Semipermanent wetlands		
Basin chemical type[a] Dominant emergents in central zone	T8 KHCO$_3$ Polygonum coccineum-Carex atherodes	T3 CaSO$_4$ Scolochloa festucacea-Carex atherodes	P1 MgSO$_4$ Typha spp.-Scirpus acutus	P8 MgHCO$_3$ Typha spp.-Scirpus acutus	P11 NaSO$_4$ Scirpus maritimus Scirpus acutus
Cyathomonas truncata				42 (10)	
Protochrysis phaeophycearum			19 (6)		
Rhodomonas sp.				417 (5)	19 (8)
R. lacustris					331 (8)
R. minuta	293 (5)	473 (6)	1985 (10)	1098 (5)	
Chlorophyta					
Actinastrum sp.	76 (7)				
Ankistrodesmus sp.	28 (6)	47 (5)	28 (5)	28 (5)	
A. braunii	28 (6)	47 (6)	19 (8,9)	30 (10)	38 (8)
A. convolutus			19 (10)		66 (8)
A. falcatus	38 (6)			9 (5)	
A. nanoselene				62 (10)	
Carteria sp.	6 (7)		19 (9)	28 (8)	
C. cordiformis				14 (8)	
Chlamydomonas sp. 1	199 (5)	848 (6)	123 (5)	497 (8)	947 (5)
C. sp. 2	350 (5)	502 (6)	682 (6)	133 (6)	137 (8)
C. sp. 3	312 (5)	473 (7)	2357 (6)	1799 (7)	133 (8)
C. sp. 4	85 (7)	227 (5)	85 (9)	9 (8)	95 (8)
C. sp. 5		114 (7)			
C. angustissima					865 (10)
Chlorella sp.					76 (8)
C. vulgaris		19 (5)	9 (5)	19 (7)	14 (8)
Chlorococcum sp. 1				19 (6,7)	
C. sp. 2				19 (6,10)	
C. humicola	331 (5)	956 (5)	322 (10)	606 (7)	114 (7)
C. infusionum			142 (9)		
Chlorogonium sp.	114 (5)		114 (10)	57 (8)	530 (8)
Closterium sp.	16 (7)		9 (8)	42 (10)	
C. sp. 1			19 (6,10)	9 (5,6)	

(Continued)

Appendix A. (Continued).

Basin chemical type[a] Dominant emergents in central zone	Seasonal wetlands		Semipermanent wetlands		
	T8 $KHCO_3$ Polygonum coccineum-Carex atherodes	T3 $CaSO_4$ Scolochloa festucacea-Carex atherodes	P1 $MgSO_4$ Typha spp.-Scirpus acutus	P8 $MgHCO_3$ Typha spp.-Scirpus acutus	P11 $NaSO_4$ Scirpus maritimus Scirpus acutus
C. sp. 2			38 (10)	9 (6)	
C. gracile				9 (7)	
Coelastrum sp.	76 (7)				
Cosmarium sp.	9 (6)				
Dictyosphaerium sp.		136 (7)			
D. ehrenbergianum	95 (5)				
Dunaliella sp.		66 (5)			57 (8)
Eudorina sp.	303 (6)				
Gloeocystis sp.					47 (8)
Mesostigma sp.				24 (6)	246 (8)
Mesotaenium sp.		19 (5,7)			
Microspora sp.		114 (7)		47 (6)	
Mougeotia sp.	9 (6)	227 (5)			
Oedogonium sp.	1969 (6)				
Oocystis sp.	57 (6)				284 (5)
Pediastrum boryanum	142 (6)				
P. tetras				38 (10)	
Pedimonas rotunda					1647 (8)
Platymonas sp.			19 (6)	19 (8)	
Pyramimonas sp.	9 (6)				7 (8)
Pyrobotrys sp.					38 (8)
Scenedesmus sp.	38 (5)			42 (10)	
S. abundans				38 (5)	
S. bijuga		189 (5)			
S. dimorphus	38 (5)				
S. longus var minutus				83 (10)	
S. quadricauda			38 (5)		
S. serratus			38 (9)	76 (8)	
Schroederia judayi			19 (6)		
S. setigera			19 (7)	9 (6,7)	9 (7)

(Continued)

Appendix A. (Continued).

Basin chemical type[a] Dominant emergents in central zone	Seasonal wetlands T8 $KHCO_3$ *Polygonum coccineum*-*Carex atherodes*	Seasonal wetlands T3 $CaSO_4$ *Scolochloa festucacea*-*Carex atherodes*	Semipermanent wetlands P1 $MgSO_4$ *Typha* spp.-*Scirpus acutus*	Semipermanent wetlands P8 $MgHCO_3$ *Typha* spp.-*Scirpus acutus*	Semipermanent wetlands P11 $NaSO_4$ *Scirpus maritimus* *Scirpus acutus*
Selenastrum sp.					38 (8)
S. *minutum*				9 (5,9)	5 (6)
Spermatozoopis exultans		57 (7)			
Sphaerocyssits schroeteri	208 (6)				
Spirogyra sp.	95 (6)		38 (10)	57 (7)	
Staurastrum sp.	76 (7)				
Stephanoptera gracilis	9 (6)				19 (8)
Tetraedron caudatum		38 (7)			
T. *trigonum*					
var *tetragonum*				19 (8)	
Treubaria sp.			19 (10)	9 (6,7)	
Ulothrix sp.	350 (6)	682 (6)			
Zygnema sp.	2595 (6)	227 (5)			
Chlorophyta resting spores			19 (8)		
Euglenophyta and Dinophyta					
Crystodinium cornifax		76 (5)			
Euglena sp.	9 (5,7)	208 (7)		38 (6)	189(5)
E. *sp*. 1	9 (7)			19 (7)	142 (5)
E. *sp*. 2	9 (7)			19 (7,8)	5 (6)
E. *sp*. 3				95 (7)	
Gymnodinium palustre	9 (7)				
Peridinium inconspicua	19 (7)			3 (8)	
Phacus sp.	9 (6)	9 (6)			
P. *caudata*	19 (6)				
P. *longicauda*		19 (6)			
Trachelomonas sp.		19 (7)		19 (7)	
Chrysophyta					
Characidiopsis sp.			9 (9)		
Chromulina sp.	843 (5)	227 (7)	123 (9)	38 (5)	71 (5)
C. *sp*. 1				133 (8)	

(Continued)

Appendix A. (Continued).

Basin chemical type[a] Dominant emergents in central zone	Seasonal wetlands T8 $KHCO_3$ Polygonum coccineum-Carex atherodes	Seasonal wetlands T3 $CaSO_4$ Scolochloa festucacea-Carex atherodes	Semipermanent wetlands P1 $MgSO_4$ Typha spp.-Scirpus acutus	Semipermanent wetlands P8 $MgHCO_3$ Typha spp.-Scirpus acutus	Semipermanent wetlands P11 $NaSO_4$ Scirpus maritimus Scirpus acutus
C. sp. 2				104 (10)	
Chrysamoeba sp.		9 (6)	9 (8,9)	9 (10)	
Chrysochromulina parva				19 (7)	
Desmarella sp.	38 (5)				
Dinobryon sp.				19 (5)	
D. acuminatum		38 (5)			
D. setularia		284 (5)		113 (5)	
Harpochytrium tenuissimum		38 (5)			
Mallomonas sp.		38 (5)			
M. akrokomas				9 (5)	
Ochromonas sp.	66 (7)	928 (6)	265 (6)	95 (6)	2414 (5)
O. sp. 1			1505 (6)	123 (8)	
O. sp. 2			331 (6)	125 (10)	
O. stellaris		511 (5)			
Ophiocytium sp.				21 (10)	
O. cochleare		57 (7)			
O. desertum var minor	9 (6)				
O. parvulum		38 (5)			
Rhyzochrysis sp.	9 (5)			5 (8)	
Synura sp.	11568 (6)	738 (6)		1420 (7)	
Tribonema sp.	1297 (6)	1435 (5)			
T. sp. 1		3332 (5)			
T. sp. 2		379 (5)			
Bacillariophyta					
Amphipleura pelucida			21 (8,10)	28 (9)	
Amphora ovalis			19 (6)	104 (10)	
A. veneta		4 (5)		9 (7)	
Cocconeis placentula			521 (9)	51 (10)	
Cyclotella meneghiniana			5 (7)	28 (5)	1041 (5)
Cylindrotheca gracilis					9 (10)

(Continued)

Appendix A. (Continued).

Basin chemical type[a] Dominant emergents in central zone	Seasonal wetlands		Semipermanent wetlands		
	T8 $KHCO_3$ Polygonum coccineum-Carex atherodes	T3 $CaSO_4$ Scolochloa festucacea-Carex atherodes	P1 $MgSO_4$ Typha spp.-Scirpus acutus	P8 $MgHCO_3$ Typha spp.-Scirpus acutus	P11 $NaSO_4$ Scirpus maritimus Scirpus acutus
Cymbella cistula			2 (5)		
C. minuta			28 (5)		
C. m. var silesica					284 (5)
Etomoneis paludosa					19 (5)
Eunotia curvata	33 (6)	6 (7)	19 (7)		
E. naegeli	2 (6)				
Fragilaria capucina			9 (6)		
F. c. var mesolepta			38 (6)	229 (10)	
F. crotonesis				28 (10)	
F. virescens		9 (5)			
Gomphonema sp.			19 (10)	9 (6)	5 (6)
G. angustatum	9 (7)		19 (6)	42 (10)	
G. gracile	28 (7)	9 (7)	57 (6)		
G. parvulum			5 (6)		9 (9)
Gyrosigma spencerii					19 (5)
Hantzschia amphioxys		19 (5)			
Melosira sp.		171 (7)			
Navicula sp.	9 (5)	5 (6)	19 (6,10)	19 (6)	19 (8)
N. accomoda		9 (6)			767 (5)
N. arvensis		9 (6)		51 (10)	
N. atomus		9 (6)			
N. capitata					9 (10)
N. cincta			9 (9)		805 (5)
N. confervacea				133 (6)	
N. cryptocephala		9 (6)		5 (8)	47 (10)
N. c. var veneta				67 (8)	214 (5)
N. cuspidata		28 (5)	19 (8)		63 (10)
N. exigua var capitata					5 (5)
N. heufleri		38 (5)	21 (5)	21 (10)	1319 (5)
N. h. var leptocephala			38 (6)	104 (8)	

(Continued)

Appendix A. (Continued).

Basin chemical type[a] Dominant emergents in central zone	Seasonal wetlands		Semipermanent wetlands		
	T8 $KHCO_3$ Polygonum coccineum-Carex atherodes	T3 $CaSO_4$ Scolochloa festucacea-Carex atherodes	P1 $MgSO_4$ Typha spp.-Scirpus acutus	P8 $MgHCO_3$ Typha spp.-Scirpus acutus	P11 $NaSO_4$ Scirpus maritimus Scirpus acutus
N. laevissima			9 (6)		
N. lanceolata		9 (6)	19 (5,7)	21 (10)	63 (10)
N. minima			19 (5)		
N. minuscula			19 (8)		
N. notha			5 (5)		9 (5)
N. pupula var rectangularis			5 (10)		
N. pygmaea					256 (5)
N. tripunctata			2 (8)	30 (10)	205 (10)
N. viridula				9 (10)	
Nitzschia sp.			9 (5)	229 (10)	180 (5)
N. acicularis			38 (8)	218 (9)	
N. amphibia		78 (5)	38 (8,10)	128 (8)	5 (8)
N. communis					58 (5)
N. denticula		2 (5)		5 (8)	
N. fonticola		2 (7)			2 (5)
N. frustulum		9 (7)			26 (5)
N. hantzschiana		19 (6)		31 (6)	123 (5)
N. hungarica					126 (10)
N. inconspicua					323 (5)
N. latens				62 (10)	
N. linearis				19 (7)	85 (5)
N. longissima					2 (5)
N. l. var reversa					5 (10)
N. minutula		21 (7)			
N. palea	47 (7)	133 (5)	57 (6)	65 (5)	183 (5)
N. paleacea	9 (5)	162 (6)	208 (6)	305 (5)	453 (5)
N. pusilla					5 (5)
N. romana		78 (7)	19 (9,10)	27 (5)	221 (5)
N. thermalis	5 (7)	78 (5)		82 (10)	

(Continued)

Appendix A. (Continued).

Basin chemical type[a] Dominant emergents in central zone	Seasonal wetlands T8 $KHCO_3$ Polygonum coccineum- Carex atherodes	 T3 $CaSO_4$ Scolochloa festucacea- Carex atherodes	Semipermanent wetlands P1 $MgSO_4$ Typha spp.- Scirpus acutus	 P8 $MgHCO_3$ Typha spp.- Scirpus acutus	 P11 $NaSO_4$ Scirpus maritimus Scirpus acutus
N. tryblionella					13 (5)
N. valdestriata					35 (5)
Pinnularia sp.		19 (5)		5 (10)	284 (5)
Plagiotropis lepidoptera var probscidea					289 (5)
Rhoicosphenia curvata					158 (10)
Rhopalodia gibba		2 (7)		24 (5)	47 (5)
R. musculus					85 (5)
Stauroneis wislouchii				9 (7)	
Synedra sp.		6 (7)	19 (5)	38 (5)	
S. famelica		561 (5)			
S. fasciculata					151 (5)
S. miniscula			9 (9)		
S. pulchella					19 (5)
S. rumpens sp.				57 (7)	
S. rumpens	66 (7)		19 (10)	9 (5,6,8)	
S. r. var fragilarioides		13 (7)			
S. ulna			9 (5)	19 (5,7)	
S. ulna var subaequalis			19 (5)	76 (7)	

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[a] LaBaugh et al. 1987.

[b] Densities are expressed as mean cells/ml (n= 3 samples/month) for the month of greatest abundance. Month of greatest abundance is in parentheses; more than one month is shown where monthly abundances were identical. Seasonal wetlands were sampled 3 times per visit each month from May through July; semipermanent wetlands were sampled 3 times per visit each month from May through October.

Appendix B. 1. Common dominance types of emergent vegetation in temporarily flooded palustrine wetland (wet meadow zones) in the Prairie Pothole Region of the Dakotas (from Stewart and Kantrud 1971, 1972; Kantrud et al. 1989).

Land use			
Grazed	Idle	Hayed	Farmed
	Freshwater		
Hordeum jubatum	*Poa palustris*	*Juncus balticus*	*Agropyron repens*
Juncus balticus	*Calamagrostis canadensis*	*Calamagrostis inexpansa*	*Echinochloa crusgalli*
Spartina pectinata	*Spartina pectinata*	*Carex lanuginosa*	*Polygonum lapathifolium*
Aster simplex	*Carex sartwellii*	*Carex praegracilis*	*Hordeum jubatum*
	Oligosaline water		
Hordeum jubatum	*Calamagrostis inexpansa*	*Juncus balticus*	*Agropyron repens*
Juncus balticus	*Spartina pectinata*	*Calamagrostis inexpansa*	*Hordeum jubatum*
Distichlis spicata	*Poa palustris*		*Artemisia biennis*
	Mesosaline water		
Distichlis spicata	*Distichlis spicata*	not seen	not seen
Hordeum jubatum	*Triglochin maritima*		
	Spartina gracilis		
	Atriplex patula		
	Muhlenbergia asperifolia		

Appendix B. 2. Common dominance types of persistent and non-persistent (asterisked) emergent vegetation in seasonally flooded palustine wetland (emergent shallow marsh zones) in the Prairie Pothole Region of the Dakotas.

Land use			
Grazed	Idle	Hayed	Farmed
		Freshwater	
Glyceria grandis Beckmannia syzigachne	Carex atherodes Sparganium eurycarpum	Carex atherodes Phalaris arundinacea	Beckmannia syzigachne Alisma plantago aquatica*
Sparganium eurycarpum Sium suave Alisma plantago-aquatica*	Phalaris arundinacea Polygonum coccineum		Alopecurus aequalis Polygonum coccineum
		Oligosaline water	
Eleocharis palustris Beckmannia syzigachne Alisma gramineum* Sium suave	Scolochloa festucacea Carex atherodes Polygonum coccineum Sagittaria cuneata*	Scolochloa festucacea Carex atherodes	Beckmannia syzigachne Sium suave Polygonum coccineum
		Mesosaline water	
Salicornia rubra* Suaeda depressa Scirpus americanus Eleocharis palustris	Scirpus americanus Pucinnelia nuttalliana	not seen	not seen

Appendix B. 3. Common dominance types of emergent vegetation in semipermanently flooded palustrine wetland (emergent deep marsh zones) in the Prairie Pothole Region of the Dakotas.

Land use			
Grazed	Idle	Hayed	Farmed
	Freshwater		
Scirpus heterochaetus *Scirpus validus* *Scirpus fluviatilis*	*Typha latifolia* *Typha angustifolia* *Typha* X *glauca*	not seen	*Scirpus fluviatilis* *Scirpus validus*
	Oligosaline water		
Scirpus acutus *Scirpus maritimus*	*Typha* X *glauca* *Typha angustifolia* *Typha latifolia* *Scirpus acutus*	not seen	*Scirpus fluviatilis*
	Mesosaline water		
Scirpus maritimus *Scirpus acutus*	*Scirpus maritimus* *Scirpus acutus*	not seen	not seen

Appendix B. 4. Common dominance types of vegetation in aquatic bed algal (A), aquatic moss and liverwort (M), rooted vascular (R) and floating vascular (F) vegetation in palustrine wetland with seasonally flooded water regime in the Prairie Pothole Region of the Dakotas.

Land use			
Grazed	Idle	Hayed	Farmed
	Freshwater		
Potamogeton gramineus (R) *Utricularia vulgaris* (R) *Potamogeton foliosus* (R) *Drepanocladus* spp. (M) *Ranunculus cymbalaria* (R) *Eleocharis acicularis* (submerged form) (R) *Riccia fluitans* (M) *Ricciocarpus natans* (M) *Lemna trisulca* (F) *Lemna minor* (F) *Ranunculus subrigidus* (R)	*Utricularia vulgaris* (R) *Drepanocladus* spp. (M) *Callitriche verna* (R) *Ranunculus sceleratus* (R) *Lemna trisulca* (F) *Lemna minor* (F) *Riccia fluitans* (M) *Ricciocarpus natans* (M)	*Lemna trisulca* (F) *Lemna minor* (F) *Riccia fluitans* (M)	*Ranunculus subrigidus* (R) *Potamogeton foliosus* (R) *Marsilea vestita* (R) *Bacopa rotundifolia* (R) *Eleocharis acicularis* (submerged form) (R) *Ranunculus sceleratus* (R)
	Oligosaline water		
Utricularia vulgaris (R) *Lemna minor* (F) *Lemna trisulca* (F) *Drepanocladus* spp. (M) *Ranunculus subrigidus* (R) *Ricciocarpus natans* (M) *Zannichellia palustris* (R) *Chara* spp. (A)	*Utricularia vulgaris* (R) *Lemna minor* (F) *Lemna trisulca* (F) *Drepanocladus* spp. (M) *Riccia fluitans* (M) *Ricciocarpus natans* (M) *Zannichellia palustris* (R) *Chara* spp. (A)	not seen	*Ranunculus subrigidus* (R) *Eleocharis acicularis* (submerged form) (R)
	Mesosaline water		
none	none	not seen	not seen

Appendix B. 5. Common dominance types of vegetation in aquatic bed algal (A), aquatic moss and liverwort (M), rooted vascular (R), and floating vascular (F) subclasses of palustrine wetland with semipermanently flooded water regime in the Prairie Pothole Region of the Dakotas.

Freshwater

Elodea *longivaginata* (R)
Spirodela *polyrhiza* (F)
Riccia *fluitans* (M)
Potamogeton *gramineus* (R)
Lemna *trisulca* (F)
Utricularia *vulgaris* (R)
Ricciocarpus *natans* (M)
Potamogeton *richardsonii* (R)

Ceratophyllum *demersum* (R)
Myriophyllum *spicatum* (R)
Drepanocladus spp. (M)
Ranunculus *subrigidus* (R)
Lemna *minor* (F)
Ranunculus *flabellaris* (R)

Oligosaline water

Hippuris *vulgaris* (R)
Ranunculus *gmelini* (R)
Ricciocarpus *natans* (F)
Callitriche *hermaphroditica* (R)
Potamogeton *zcsteriformis* (R)
Potamogeton *pusillus* (R)
Lemna *trisulca* (F)
Utricularia *vulgaris* (R)
Potamogeton *richardsonii* (R)
Ceratophyllum *demersum* (R)
Myriophyllum *spicatum* (R)

Drepanocladus spp. (M)
Ranunculus *subrigidus* (R)
Lemna *minor* (F)
Zannichellia *palustris* (R)
Chara spp. (A)
Potamogeton *pectinatus* (R)

Mesosaline water

Zannichellia *palustris* (R)
Chara spp. (A)
Potamogeton *pectinatus* (R)
Ruppia *maritima* (R)

Appendix C. 1. Common emergent hydrophytes of palustrine wetlands with temporarily flooded moisture regimes (wet meadows) in the Prairie Pothole Region of the Dakotas, arranged according to increasing maximum observed tolerance of dissolved salts (from Smeins 1967; Disrud 1968; Kantrud et al. 1989).

Species	Specific conductivity (mS/cm)[a]		
	Mean	Min.	Max.
Vernonia fasciculata	0.1	0.1	0.2
Agrostis stolonifera	0.2	--	--
Lycopus americanus	0.3	--	--
Potentilla rivalis	0.3	--	--
Carex stipata	0.4	--	--
Equisetum arvense	0.4	--	--
Juncus interior	0.4	0.3	0.9
Aster sagittifolius	1.0	--	--
Plantago major	1.0	--	--
Potentilla norvegica	0.3	0.1	1.1
Juncus dudleyi	0.4	0.3	1.3
Carex buxbaumii	1.2	1.0	1.4
Lysimachia hybrida	0.1	0.1	1.6
Carex vulpinoidea	1.0	0.1	1.7
Ranunculus macounii	1.1	0.1	2.1
Rumex mexicanus	0.5	0.1	2.2
Juncus bufonius	2.3	--	--
Cirsium arvense	2.5	--	--
Bidens cernua	1.5	0.7	2.5
Helenium autumnale	1.5	0.5	2.5
Carex praegracilis	0.3	0.1	3.0
Echinochloa crusgalli	1.3	0.5	3.2
Carex laeviconica	1.5	0.1	3.2
Rorippa islandica	1.7	0.1	3.2
Poa palustris	1.4	Tr.[b]	3.4
Stachys palustris	1.8	0.1	3.6
Calamagrostis canadensis	1.4	0.4	3.8
Carex sartwellii	1.5	0.4	3.8
Lycopus asper	1.9	0.4	4.4
Epilobium glandulosum	1.5	0.5	4.7
Mentha arvensis	1.6	0.1	4.9
Apocynum sibiricum	1.8	0.4	5.0
Eleocharis compressa	2.0	0.7	5.0
Carex tetanica	2.0	0.9	5.5
Potentilla anserina	1.6	0.1	6.0
Boltonia asteroides	1.4	0.1	6.8
Carex lanuginosa	2.0	0.1	9.1
Teucrium occidentale	3.1	0.2	9.1
Aster hesperius	2.4	0.4	9.8
Juncus torreyi	1.7	0.2	10.0
Aster simplex	1.8	0.1	16.1
Calamagrostis inexpansa	2.6	Tr.	17.6
Juncus balticus	3.3	0.1	20.1

(Continued)

Appendix C. 1. (Concluded).

Species	Specific conductivity (mS/cm)[a]		
	Mean	Min.	Max.
Spartina gracilis	9.0	0.7	20.1
Plantago eriopoda	9.8	1.0	20.1
Sonchus arvensis	5.2	0.5	20.8
Spartina pectinata	3.0	Tr.	33.5
Muhlenbergia asperifolia	11.0	0.7	38.5
Hordeum jubatum	7.8	Tr.	48.6
Triglochin maritima	12.5	0.7	50.9
Distichlis spicata	17.0	0.5	76.4
Atriplex patula	23.0	6.9	76.4

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[a] Underlined means (Disrud 1968; Kantrud et al. 1989) indicate surface water measurements in wetlands where the species reached peak abundance; underlined ranges (ibid) are for instances where the species occurred in waters of greater or lesser salinity than that recorded by Smeins (1967).

[b] Indicates measurements <0.05 mS/cm.

Appendix C. 2. Common emergent hydrophytes of palustrine wetlands with seasonally flooded (SE) (shallow-marsh zones), semipermanently flooded (SP) (deep-marsh zones), and saturated (SA) (fen zones) moisture regimes in the Prairie Pothole Region of the Dakotas, arranged according to increasing maximum observed tolerance of dissolved salts (from Smeins 1967; Disrud 1968; Kantrud et al. 1989).

Species	Water regime	Specific conductivity (mS/cm)[a]		
		Mean	Min.	Max.
Equisetum fluviatile	SE	0.3	--	--
Galium trifidum	SA	0.3	--	--
Scutellaria galericulata	SA	0.3	--	--
Impatiens biflora	SA	0.4	--	--
Mimulus ringens	SA	0.6	--	--
Eupatorium maculatum	SA	0.7	--	--
Sagittaria cuneata	SE	0.7	--	--
Glyceria striata	SA	0.8	--	--
Ranunculus gmelini	SA	0.8	--	--
Asclepias incarnata	SA	0.8	0.8	0.9
Parnassia glauca	SA	0.9	--	--
Glyceria borealis	SE	1.0	--	--
Salix interior	SA	0.4	0.3	1.7
Carex lacustris	SA	1.4	0.9	1.7
Solidago graminifolia	SA	0.8	0.1	2.1
Polygonum amphibium	SE	0.6	0.1	2.2
Scirpus atrovirens	SA	1.0	0.5	2.2
Cicuta maculata	SA	1.4	0.5	2.2
Eriphorum angustifolium	SA	1.8	0.5	2.2
Carex rostrata	SA	1.1	0.2	2.6
Polygonum coccineum	SE	1.3	Tr.[b]	3.4
Phalaris arundinacea	SE	1.6	0.1	3.8
Carex aquatilis	SA	1.6	0.3	3.8
Lysimachia thrysiflora	SA	1.7	0.5	3.8
Glyceria grandis	SE	0.7	Tr.	4.0
Sium suave	SE	1.8	0.1	4.0
Scirpus heterochaetus	SP	1.4	0.1	4.2
Alopecurus aequalis	SE	1.1	0.1	4.5
Sparganium eurycarpum	SE	1.8	Tr.	4.6
Eleocharis acicularis	SE	1.5	0.1	5.8
Scirpus validus	SP,SA	1.8	0.2	6.2
Typha X *glauca*	SP	0.8	0.1	6.6
Sagittaria cuneata	SE	1.8	0.1	6.7
Scirpus fluviatilis	SP	1.9	0.3	6.7
Alisma gramineum	SE	2.0	0.3	6.7
Carex atherodes	SE	2.0	Tr.	8.5
Ranunculus sceleratus	SE	3.6	0.1	8.5
Beckmannia syzigachne	SE	1.5	Tr.	9.5
Alisma plantago-aquatica	SE	1.8	Tr.	9.5
Ranunculus cymbalaria	SE	3.5	0.6	9.5
Scolochloa festucacea	SE	3.4	0.1	12.1
Phragmites australis	SA	3.5	0.5	12.4
Typha latifolia	SP,SA	2.1	0.1	13.6
Typha angustifolia	SP	3.4	0.4	13.6

(Continued)

Appendix C.2. (Concluded).

Species	Water regime	Specific conductivity (mS/cm)[a]		
		Mean	Min.	Max.
Eleocharis palustris	SE	2.7	*0.1*	*14.5*
Scirpus nevadensis	SE	15.7	12.0	*20.5*
Scirpus acutus	SP	4.3	*0.2*	*24.0*
Suaeda depressa	SE	24.0	*5.0*	*66.0*
Scirpus americanus	SE	4.9	*0.5*	*70.0*
Scirpus maritimus	SP	10.3	*0.8*	76.4
Puccinellia nuttalliana	SE	20.0	*1.4*	76.4

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[a] Underlined means (Disrud 1968; Kantrud et al. 1989) indicate surface water measurements in wetlands where the species reached peak abundance; underlined ranges (ibid) are for instances where the species occurred in waters of greater or lesser salinity than that recorded by Smeins (1967).

[b] Indicates measurements <0.05 mS/cm.

Appendix C. 3. Common submersed and floating aquatic plants of the Prairie Pothole Region of the Dakotas arranged according to increasing maximum observed tolerance of dissolved salts (from Smeins 1967; Disrud 1968; Kantrud et al. 1989).

Species	Specific conductivity (mS/cm)[a]		
	Mean or single measurement	Min.	Max.
Myriophyllum pinnatum	0.1	--	--
Nuphar variegatum	0.4	--	--
Najas flexilis	0.4	--	--
Elodea canadensis	0.4	--	--
Potamogeton friesii	0.6	0.3	1.0
Myriophyllum verticillatum	1.1	--	--
Potamogeton gramineus	0.8	0.1	1.2
Callitriche palustris	0.3	0.1	1.7
Hippuris vulgaris	0.7	0.5	2.3
Callitriche hermaphroditica	1.2	0.5	2.5
Ranunculus flabellaris	2.0	0.4	2.5
Potamogeton zosteriformis	1.0	0.3	2.8
Spirodela polyrhiza	1.5	0.6	3.0
Ricciocarpus natans	2.2	0.3	3.2
Drepanocladus spp.	1.2	0.1	3.3
Potamogeton vaginatus	3.3	--	--
Potamogeton richardsonii	1.7	0.3	4.0
Ranunculus subrigidus	1.4	0.2	4.5
Riccia fluitans	2.1	0.1	4.7
Ceratophyllum demersum	2.1	0.1	5.1
Potamogeton pusillus	2.1	0.1	6.7
Myriophyllum spicatum	2.2	0.2	6.7
Utricularia vulgaris	2.7	0.1	8.1
Lemna minor	3.1	0.1	10.9
Lemna trisulca	3.2	0.1	13.9
Ruppia maritima var. *occidentalis*	4.1	0.6	14.2
Zannichellia palustris	4.8	0.3	25.0
Chara spp.	2.2	0.3	42.0
Potamogeton pectinatus	6.5	0.4	60.0
Ruppia maritima var. *rostrata*	36.1	5.5	66.0

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[a] Underlined means (Disrud 1968; Kantrud et al. 1989) indicate surface water measurements in wetlands where the species reached peak abundance; underlined ranges (ibid) are for instances where the species occurred in waters of greater or lesser salinity than that recorded by Smeins (1967).

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The shallow basin wetlands of the Dakotas form the bulk of the portion of the Prairie Pothole Region lying within the United States. This region produces a large proportion of North America's waterfowl and other prairie dwelling marsh and aquatic birds. The Prairie Pothole Region is also a major world supplier of cereal grains. Consequently, wetlands in the region are often drained for crop production or are otherwise cropped when water conditions permit. Prairie basin wetlands vary greatly in their ability to maintain surface water and in their water chemistry, which varies from fresh to polysaline. In addition, these wetlands are affected by a variety of agricultural land uses and practices, including pasture, cultivation, mechanical forage removal, idle conditions, and burning. It is important to understand how these factors operate in prairie basin wetlands, since they greatly affect the plant and animal communities in these basins.

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